

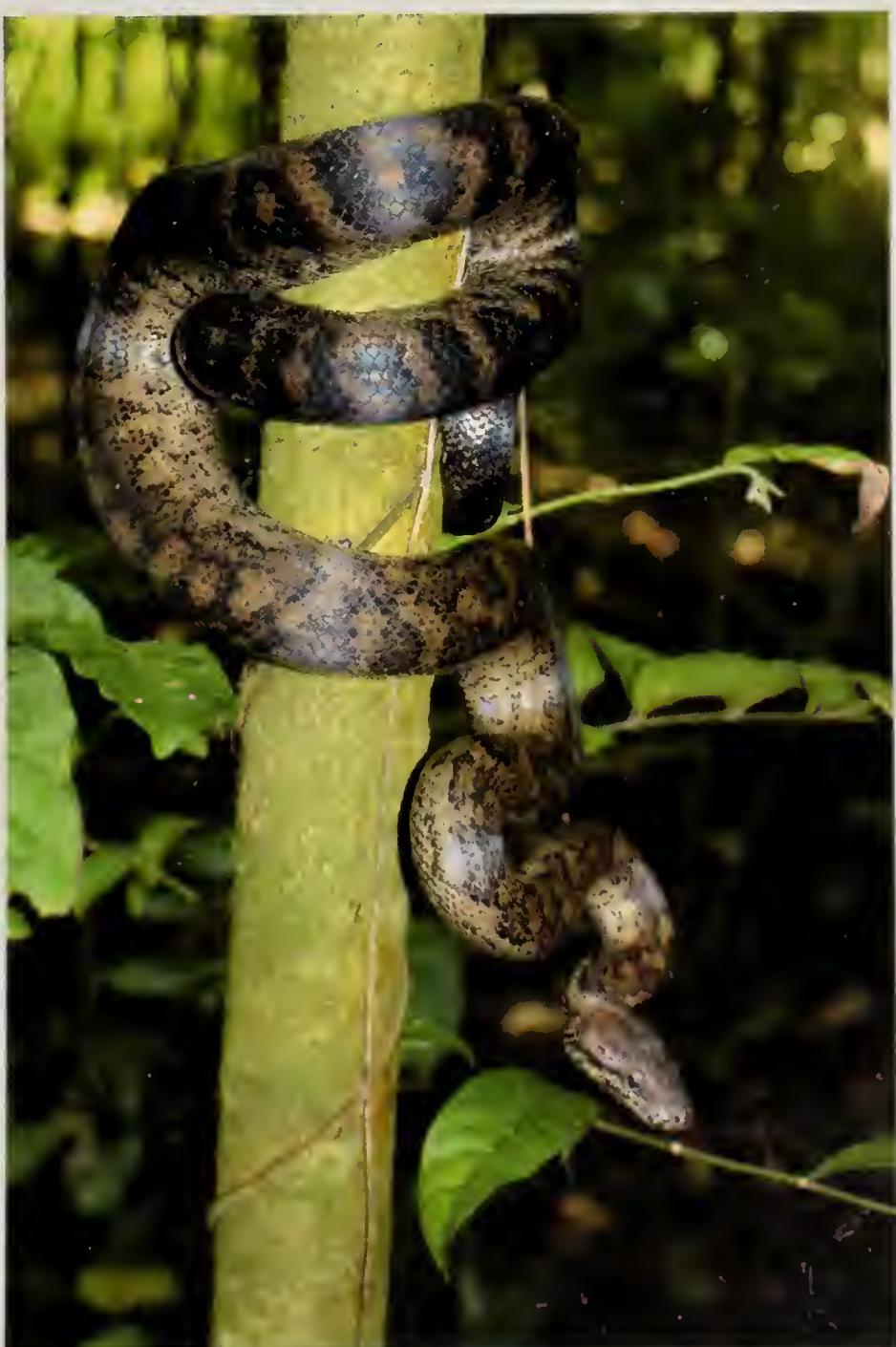
# Bulletin of the **Museum of Comparative Zoology**

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Boas of the World (Superfamily Booidae): A Checklist with Systematic, Taxonomic, and Conservation Assessments

R. Graham Reynolds and Robert W. Henderson



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# BOAS OF THE WORLD (SUPERFAMILY BOOIDAE): A CHECKLIST WITH SYSTEMATIC, TAXONOMIC, AND CONSERVATION ASSESSMENTS

R. GRAHAM REYNOLDS<sup>1</sup> AND ROBERT W. HENDERSON<sup>2</sup>

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**ABSTRACT.** The booid snakes (superfamily Booidae) are a near-circumglobally distributed group of macrostomian alethinophidian squamates, and several lineages are of significant conservation concern. A number

of taxonomic changes have occurred among the superfamily Booidae over the last decade, including the resurrection and description of new families, elevation of a genus, elevation of 13 species, and the discovery of a new species. Here, we aim to synthesize existing knowledge of booid diversity, systematics, and conservation status. We provide a comprehensive checklist of all 66 species and 33 subspecies of booid snakes recognized herein, distributed among 14 genera and six families. For each species and subspecies, we evaluate taxonomy, distribution, type specimens, and conservation status.

**Key words:** Boidae, Conservation Status, Distribution, Phylogeny, Nomenclature, Type Specimen

## INTRODUCTION

The first checklist of the boid (family Boidae Gray, 1825) snakes by Stull (1935) recognized 66 taxa (39 species, 27 subspecies) among 15 genera of what was then considered Boinae Gray 1825, a subfamily of Boidae (which also included Pythoninae and *Loxocemus*). Since that time, our understanding of the diversity and systematics of this group has changed a great deal (Table 1). For example, Stull's (1935) list of Boinae included the genera *Tropidophis*, *Bolyeria*, and *Casarea*; they are now considered representatives of distinct families (Tropidophiidae and Bolyeriidae) of henophidian snakes (e.g., Reynolds et al., 2014). Removing the taxa presently excluded from the booids, Stull's (1935) treatment included 30 species among 12 genera. In the

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TABLE 1. THE NUMBER OF GENERA, SPECIES, AND SUBSPECIES TREATED IN CHECKLISTS OR SYSTEMATIC ACCOUNTS OF THE BOOIDAE SINCE 1935.

| Source                 | Genera | Species | Subspecies |
|------------------------|--------|---------|------------|
| Stull, 1935            | 12     | 30      | 33         |
| Stimson, 1969          | 14     | 39      | 58         |
| Kluge, 1991            | 8      | 25      | —          |
| McDiarmid et al., 1999 | 8      | 41      | —          |
| Wallach et al., 2014   | 13     | 59      | —          |
| This paper             | 14     | 66      | 33         |

decades following the publication of Stull's list, boid systematics were frequently revised and rearranged. Stimson (1969) published an updated checklist, recognizing 14 boid genera, 39 species, and 58 subspecies, including *Xenboa* (=*Corallus*) *cropanii*, a genus no longer recognized. Kluge (1991) provided a de facto checklist of boids; he recognized 25 species among 8 genera (including *Xenboa*). Since Kluge (1991), major reorganizations of boid genera have occurred over the last 10 years (e.g., Passos and Fernandes, 2008; Rivera et al., 2011; Reynolds et al., 2013a). Recent larger scale, species-level, molecular phylogenies (Pyron et al., 2013; Reynolds et al., 2014) have further suggested a historically incomplete representation of booid lineages and some discordance between taxonomy and phylogenetic relationships. These authors made a number of taxonomic rearrangements and suggestions, and subsequent work has accepted, expanded, or rejected these recommendations (Reeder et al., 2015; Figueroa et al., 2016; Streicher and Wiens, 2016; Zheng and Wiens, 2016; Uetz et al., 2017). Beginning with higher level systematics, these molecular phylogenies demonstrated inconsistencies in the placement of the booid family Calabariidae with respect to other alethinophidian lineages (Pyron et al., 2013; Reynolds et al., 2014; Harrington and Reeder, 2017). To resolve this, Pyron et al. (2014) erected additional booid families to accommodate distinct monophyletic lineages, simultaneously alleviating taxonomic issues related to phylogenetic uncertainty

deeper in the booid phylogeny (the paraphyly of Boidae Gray 1825 given inconsistent placement of Calabariidae). This led to a narrowed definition of the Boidae to include only the New World genera *Boa*, *Chilabothrus*, *Corallus*, *Epicrates*, and *Eunectes*, all derived from an ancestral lineage in the Paleogene (Hsiang et al., 2015). Newly recognized families include Sanzinidae (*Acrantophis* and *Sanzinia*), Erycidae (*Eryx*), Charinidae (*Charina*, *Exiliboa*, *Lichanura*, *Ungaliophis*), and Candoiidae (*Candoia*). Not all workers embrace these changes, instead opting to remain agnostic regarding potential paraphyly until further phylogenetic relationships are worked out. Nevertheless, the recognition of families representing geographically, morphologically, and evolutionarily distinct lineages provides stability in the systematics and taxonomy of the group now and into the future, despite ongoing uncertainty in some phylogenetic relationships (Pyron et al., 2014). Continued efforts are ongoing to resolve some of the more challenging nodes in the booid phylogeny, including the application of genomic-scale data (e.g., Ruane and Austin, 2017) that suggests Calabariidae might be sister to the rest of the extant booids (Fig. 1).

Additional recent taxonomic changes within the Booidae include the resurrection of the genus *Chilabothrus* for some West Indian boids. Thirteen new species of booids have also recently been recognized, largely resulting from phylogenetic studies of molecular data (Passos and Fernandes, 2008; Wood et al., 2008; Reynolds et al., 2013a, 2014; Card et al., 2016; Reynolds et al., 2018) or newly discovered species (Reynolds et al., 2016a).

Members of the superfamily Booidae are of Gondwanan origins (Noonan and Chippindale, 2006) and are distributed nearly circumglobally (Fig. 2). Major lineages are present in the Western hemisphere (Boidae + Charinidae; 43 species), Africa (Calabariidae + Erycidae; four species),



Figure 1. Time-calibrated phylogeny of booid snakes based on an 11-gene supermatrix (after Reynolds et al., 2014). Calibration of the age of crown snakes was set to 145 mya (close to the mean inferred in Zheng and Weins, 2016), and the tree was inferred using the Bayesian algorithm implemented in the program BEAST v.1.8 (Drummond et al., 2012). This figure is therefore merely intended to show an approximation of divergence times and evolutionary relationships among booid genera to illustrate concepts discussed in the text.

Eurasia (Erycidae; 10 species), Madagascar (Sanziniidae; four species), and Oceania exclusive of Australia (Candoiidae; five species). Fossil booids are known from

regions where they do not presently have extant representatives, such as Eastern North America (Holman, 1998; Mead and Schubert, 2013) and Western Europe

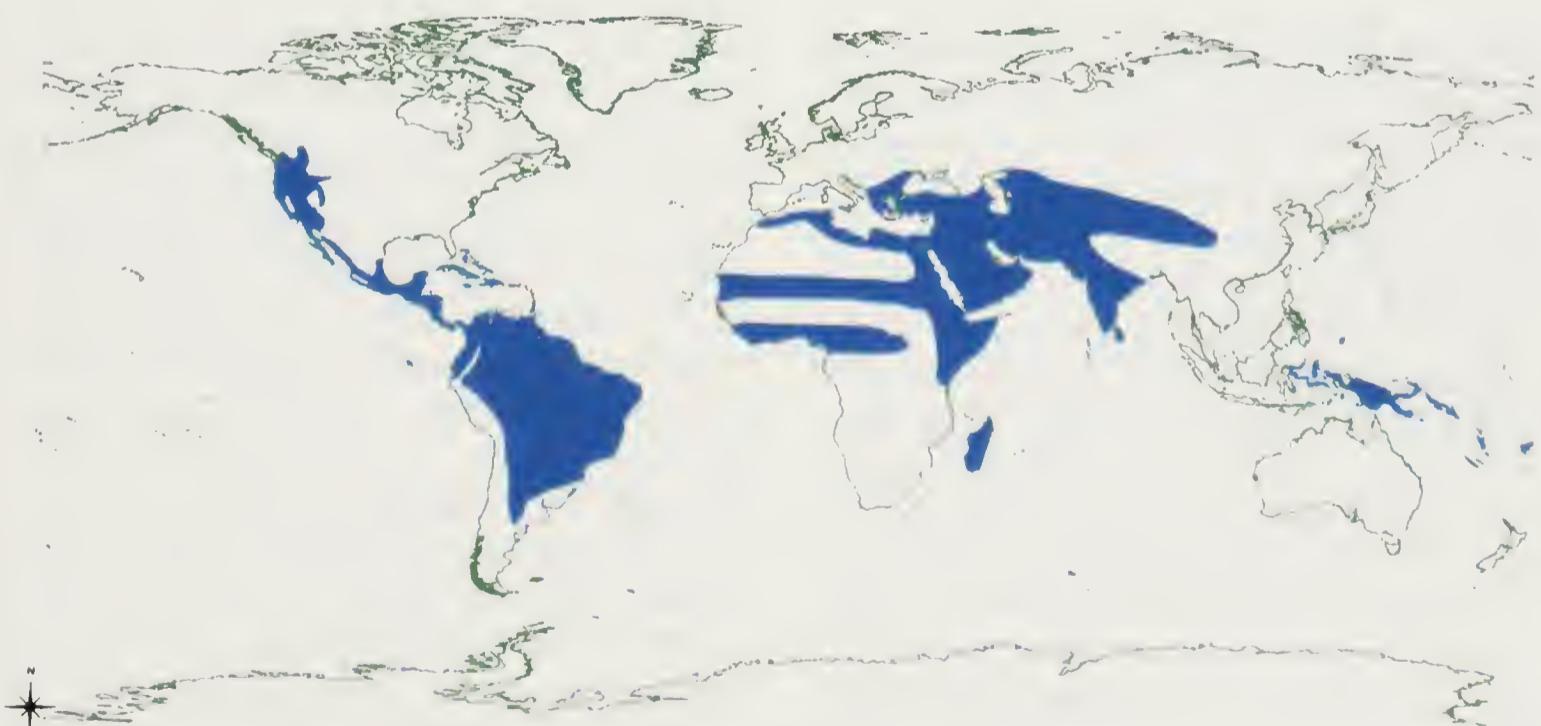


Figure 2. Approximate global distribution of booid snakes in blue.

outside the distal Balkan Peninsula (Szynalar, 1991, 2009).

Booid taxonomy and systematics have experienced a considerable amount of flux over the last several decades, motivating a re-evaluation of the current state of taxonomy and diversity within the superfamily (*sensu* Pyron et al., 2014). This is especially relevant given the largely unknown conservation status of many of the world's booid snakes (Böhm et al., 2013; IUCN 2017) and the worrying prospects of some of those that have been evaluated (Tzika et al., 2008; Reynolds, 2011; Reynolds et al., 2016a; this work). Below, we provide generic and species accounts for all recognized species and subspecies of booids. For each account, we provide the taxonomic authority, a brief taxonomic history, type specimens, distribution, and conservation information for the species and subspecies. Unless we saw a specific need to do so, our checklist does not repeat lengthy synonymies that are available elsewhere (e.g., the excellent McDiarmid et al., 1999). All but one species of boa (superfamily Booidae, formerly family Boidae) are protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Six species are listed under CITES Appendix I and are noted below; the rest are listed under CITES Appendix II. Additional conservation designations have been assigned to some taxa, which are also noted. Our taxonomic presentation largely follows from McDiarmid et al. (1999), Wallach et al. (2014), Pyron et al. (2014), and Uetz et al. (2017), and these references contain full taxonomic histories for these species. We re-evaluate standing taxonomy from these sources and make several suggestions for taxonomic revision, recognizing 14 genera (Fig. 1), 66 species, and 33 subspecies of booid snakes. We have opted not to assign common names to the various species. We were uncomfortable imposing English language names because the majority of the species in this checklist occur in countries in

which the native language is not English. A representative photograph is provided for each genus.

## SPECIES ACCOUNTS

### FAMILY BOIDAE GRAY, 1825

#### *Boa* Linnaeus, 1758

Apart from a brief visit by the Malagasy boids (*Acrantophis* and *Sanzinia*), *Boa* or *Constrictor* has been considered a monotypic genus for over 100 years (1906–2009). Five species of *Boa* are now recognized based on morphological data, molecular data, or both. The genus has a vast mainland distribution, from northern Mexico to southern South America in Argentina, Paraguay, and Brazil, as well as continental and oceanic (St. Lucia and Dominica in the Lesser Antilles) islands. Species of *Boa* occur in a wide array of habitats, ranging from near-desert circumstances to tropical rainforests, and from sea level to about 2,000 m. They range in size from dwarfed island populations (of *B. imperator*) to >4.0 m in some South American *B. constrictor*. Although largely ground dwelling, they are capable of arboreal activity and will hunt in trees. Species of *Boa* take a wide taxonomic array of prey, including lizards, birds, and mammals (including marsupials, rodents, carnivores, bats, and primates). In recent years, species of *Boa* have been accidentally or purposely introduced to geographic areas where they formerly did not occur, with the potential of negatively affecting wildlife native to those areas (e.g., Quick et al., 2005; Romero-Nájera et al., 2007). *Boa* is sister to a clade comprising *Chilabothrus* + *Corallus* + *Epicrates* + *Eunectes*.

#### *Boa constrictor* Linnaeus, 1758

**Taxonomy.** Originally described as *Boa constrictor*, this species has had a long taxonomic history placed in either *Boa* or *Constrictor*. Many names have been assigned to those two genera, and until recently, all have been placed into synony-

TABLE 2. LIST OF MUSEUM ABBREVIATIONS USED IN THE TEXT WITH CORRESPONDING INSTITUTION AND LOCATION.

| Code  | Institution Name  | Location                        |
|-------|---|---------------------------------|
| AMNH  | American Museum of Natural History                          | New York, New York, USA         |
| AMS   | Australian Museum Sydney                                    | Sydney, Australia               |
| ANSP  | Academy of Natural Sciences of Philadelphia                 | Philadelphia, Pennsylvania, USA |
| BINH  | British Museum of Natural History                           | London, England                 |
| CM    | Carnegie Museum   | Pittsburgh, Pennsylvania, USA   |
| IB    | Instituto Butantan  | São Paulo, Brazil               |
| KUHH  | Kansas University Herpetological Collection                 | Lawrence, Kansas, USA           |
| LSUMZ | Louisiana State University Museum of Zoology                | Baton Rouge, Louisiana, USA     |
| MCZ   | Museum of Comparative Zoology                               | Cambridge, Massachusetts, USA   |
| MNIIN | Museum National d'Histoire Naturelle, Paris                 | Paris, France                   |
| MNKHU | Museum of Nature of the Kharkiv National University         | Kharkiv, Ukraine                |
| MSNM  | Museo Civico di Storia Naturale, Milano                     | Milan, Italy                    |
| NMBA  | Naturhistorisches Museum Basel                              | Basel, Switzerland              |
| NRM   | Naturhistoriska Riksmuseet                                  | Stockholm, Sweden               |
| SDSNH | San Diego Natural History Museum                            | San Diego, California, USA      |
| UMMZ  | University of Michigan Museum of Zoology                    | An Arbor, Michigan, USA         |
| USNM  | US National Museum of Natural History                       | Washington, DC, USA             |
| ZFMK  | Zoologisches Forschungsinstitut und Museum Alexander Koenig | Bonn, Germany                   |
| ZISP  | Zoological Institute, Russian Academy of Sciences           | St. Petersburg, Russia          |
| ZIUU  | Uppsala Universitet Zoologiska Museet                       | Uppsala, Sweden                 |
| ZMB   | Universität Humboldt, Zoologisches Museum                   | Berlin, Germany                 |
| ZMH   | Zoologisches Museum für Hamburg                             | Hamburg, Germany                |
| ZMUC  | Universitets Kobenhavn, Zoologisk Museum                    | Copenhagen, Denmark             |
| ZSI   | Zoological Survey of India                                  | Kolkata, India                  |
| ZSM   | Zoologische Staatssammlung München                          | Munich, Germany                 |

my or have been described originally as subspecies or have been relegated to subspecific rank. Only recently has *B. constrictor* been partitioned into multiple species (Henderson and Powell, 2009; Hynková et al., 2009; Reynolds et al., 2014; Suárez-Atilano et al., 2014, 2017; Card et al., 2016). See McDiarmid et al. (1999) for a more complete synonymy. A number of subspecific epithets continue to be used by some sources (e.g., Uetz et al., 2017) but are not recognized by others (this work). This is partly owing to the preliminary molecular phylogenetic surveys of the genus, the unknown provenance of some samples used in these analyses (e.g., Hynková et al., 2009), and lack of a comprehensive morphological and molecular study of the genus. For example, *B. c. amarali* Stull 1932 is an epithet used to refer to populations from southern Brazil, possessing lower numbers of scale rows, ventrals, and caudals (Stull, 1932), but is not supported as distinct in other analyses

(Hynková et al., 2009). We recognize four subspecies.

**Type Specimens.** Two syntypes, NRM 10 and NRM 20001, a third syntype is presumed lost (McDiarmid et al., 1999). Type locality “Indiis” (in error, *fide* Peters and Orejas-Miranda, 1970).

**Distribution.** South America: Colombia, Ecuador, Peru, Venezuela (including Isla Margarita), Guyana, Suriname, French Guiana, Brazil, Bolivia, Argentina, and Paraguay; Trinidad, Tobago, Puerto Rico (introduced; Reynolds et al., 2013b), and Aruba (introduced; Bushar et al., 2015).

**Conservation Status.** This species has not received an IUCN Red List assessment.

#### *Boa constrictor constrictor* Linnaeus, 1758

**Taxonomy.** Originally described as a full species, but subsequently relegated to subspecies rank with the description of multiple taxa that were either described as full species of *Boa* or *Constrictor* and then relegated to a subspecies of *B.* or *C.*

*constrictor*, or originally described as subspecies of *B. constrictor* or *C. constrictor*. See McDiarmid et al. (1999) for a more thorough synonymy.

**Type Specimens.** See *Boa constrictor* account.

This taxon has not received an IUCN Red List assessment, but it has commercial appeal among boid hobbyists.

#### *Boa constrictor longicauda* Price & Russo, 1991

**Taxonomy.** Described as a subspecies of *Boa constrictor* based on tail length, color pattern, and scale characters.

**Type Specimen.** The holotype is a subadult male (MCZ R176002) collected “east of Tumbes, Tumbes Province, Peru” (Price and Russo, 1991:32). Later in the description by (Price and Russo, 1991), the holotype is described as a small adult.

**Distribution.** Known only from Tumbes Province in coastal Peru.

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Boa constrictor occidentalis* Philippi, 1873

**Taxonomy.** Originally described as *Boa occidentalis*; Ihering (1910) subsumed it to a subspecies within *Constrictor constrictor*; Forcart used the trinomial *Boa c. occidentalis*. Bezerra de Lima (2016) considered *B. occidentalis* a distinct lineage within the *B. constrictor* complex.

**Type Specimen.** The type is unlocated (McDiarmid et al., 1999); type locality (fide Stimson, 1969) “Provinces Mendoza and San Juan, Argentina.”

**Distribution.** Paraguay and Argentina, between the Andes (Río Colorado) and the ríos Paraguay and Paraná, south to Mendoza Province, Argentina (Cei, 1993; Chiaraviglio et al., 1998).

**Conservation Status.** This taxon has not received an IUCN Red List assessment; it is, however, listed under CITES Appendix I



Figure 3. *Boa imperator* from Cayos Cochinos, Honduras. Photo by R. Graham Reynolds, University of North Carolina Asheville.

(i.e., the most endangered and threatened with extinction).

#### *Boa constrictor ortonii* Cope, 1878

**Taxonomy.** Originally described as *Boa ortonii*; relegated to a subspecies of *Constrictor constrictor* by Schmidt and Walker (1943); Stimson (1969) was first to use the trinomial *B. c. ortonii*.

**Type Specimen.** ANSP 11402, “from Chilete, near Pacasmayo, 3000 feet [915 m] above the sea,” Peru (Cope, 1878:35).

**Distribution.** Peru: regions of Piura, Lambayeque, Cajamarca, Amazonas, and la Libertad west of the Andes, and along the Río Marañón valley at elevations of 0–2000 m (Koch, 2013).

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Boa imperator* Daudin, 1803

**Taxonomy.** Originally described as a full species, it was subsequently subsumed to a subspecies of *Constrictor constrictor* by Ihering (1910); Forcart (1951) recognized it as *B. c. imperator*; based on molecular data, a number of authors (Hynková et al., 2009; Reynolds et al., 2014; Suárez-Atilano et al., 2014, 2017; Card et al., 2016) suggested elevating it to full species. Bezerra de Lima (2016) considered *B. imperator* a distinct lineage within the *B.*

*constrictor* complex, and this species is being recognized in contemporary treatments (e.g., Johnson et al., 2015; García-Padilla et al., 2016). Two subspecies are recognized.

**Type Specimen.** In the MNHN, but not definitely identifiable (J. Guibé in Stuart, 1963). Type locality “l’Amerique méridionale principalement au Mexique” was subsequently restricted to Córdoba, Veracruz, Mexico, by Smith and Taylor (1950); however, Dunn and Saxe (1950) favored the Colombian Chocó as the type locality.

**Distribution.** Southeastern Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and northwestern Colombia; includes many islands off the Caribbean/Atlantic and Pacific coasts of several of those countries. Introduced to Cozumel Island (Vázquez-Domínguez et al., 2012) and St. Croix (Golden, 2017).

**Conservation Status.** This species has not received an IUCN Red List assessment. Using IUCN Red List criteria, Acevedo et al. (2010) categorized this species as of Least Concern in Guatemala, as did Greenbaum and Komar (2010) for El Salvador, Townsend and Wilson (2010) for Honduras, and Sosa et al. (2010) for Costa Rica; Jaramillo et al. (2010) gave *B. imperator* an assessment of Vulnerable for Panama. Stafford et al. (2010) gave it a low Environmental Vulnerability Score for Belize.

#### *Boa imperator imperator* Daudin, 1803

**Taxonomy.** See *Boa imperator* above.

**Type Specimen.** See *Boa imperator* above.

**Distribution.** Southeastern Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and northwestern Colombia; includes many islands off the Caribbean/Atlantic and Pacific coasts of several of those countries (excluding the Islas de las Perlas in the Gulf of Panama). Introduced to Cozumel Island (Vázquez-

Domínguez et al., 2012) and St. Croix (Golden, 2017).

**Conservation Status.** This taxon has not received an IUCN Red List assessment. Certain populations of *B. i. imperator* on the Bay Islands of Honduras have been severely affected by poaching for the pet trade, though some populations have recovered after protection in the Cayos Cochinos Archipelago Natural Marine Monument (Wilson and Cruz Diaz, 1993; Reed et al., 2007; Montgomery et al., 2015).

#### *Boa imperator sabogae* (Barbour, 1906)

**Taxonomy.** Originally described as *Epicrates sabogae*. Barbour and Loveridge (1929) considered it a subspecies of *Constrictor constrictor*; Forcart (1951) used *Boa c. sabogae*; Reynolds et al. (2014), recognizing *B. imperator* as a full species, used the trinomial *B. i. sabogae*.

**Type Specimens.** Description based on two syntypes (MCZ R6986) from Saboga Island, one of the Islas de las Perlas off the Pacific coast of Panama.

**Distribution.** Apparently restricted to Isla Saboga and Isla San José, Islas de las Perlas, Gulf of Panama, but likely found on other islands in the archipelago.

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Boa nebulosa* (Lazell, 1964)

**Taxonomy.** Originally described as a subspecies of *Constrictor constrictor*, it was elevated to species status by Henderson and Powell (2009) based on scale and pattern characters provided by Lazell (1964), as well as geographic isolation. Before Lazell’s description, the boa population on Dominica was referred to as *B. diviniloqua* Günther (1888) and then fell under the taxonomic umbrella of the St. Lucia population (*Constrictor orophias*; e.g., Barbour, 1930, 1937). Bezerra de Lima (2016) considered *B. nebulosa* a distinct

lineage within the *B. constrictor* complex. No subspecies are recognized.

**Type Specimen.** The holotype (MCZ R65493) is an adult female from Woodford Hill, Dominica.

**Distribution.** Endemic to the Lesser Antillean island of Dominica, West Indies.

**Conservation Status.** This species has been assessed as Least Concern based on IUCN Red List criteria, though that assessment is in review. Its distribution is limited to a small ( $790 \text{ km}^2$ ) island and should certainly be assessed as Vulnerable. These boas are killed for the “medicinal” oil rendered from their fat and because they prey on domestic chickens (Henderson and Powell, 2009).

#### *Boa orophias* Linnaeus, 1758

**Taxonomy.** Originally described as a full species by Linnaeus, it was placed in the synonymy of *Constrictor diviniloquus* (or *diviniloqua* or *diviniloquax*) by Laurenti (1768) and subsequently by Duméril and Bibron (1844). Barbour (1914) regarded it as full species (*C. orophias*), but it was subsequently downgraded to subspecies by Amaral (1929). It was again elevated to species status by Stull (1935) as *C. orophias*, but Lazell (1964) considered it a subspecies of *C. constrictor*, as did Peters and Orejas-Miranda (1970; as *Boa c. orophias*). It was then given species rank by Henderson and Powell (2009) based on scale and pattern characters in Lazell (1964), as well as geography. Bezerra de Lima (2016) considered *B. orophias* a distinct lineage within the *B. constrictor* complex. No subspecies are recognized.

**Type Specimen.** An unnumbered specimen in the Museum de Geer (Andersson, 1899). Type locality not given in original description; Lazell (1964) restricted it to Praslin, St. Lucia.

**Distribution.** Endemic to the Lesser Antillean island of St. Lucia in the West Indies.

**Conservation Status.** This species has been assessed as Endangered based on IUCN Red List criteria, though that assessment is in review. The species has a limited distribution on a small ( $604 \text{ km}^2$ ) island and is often killed because of its superficial resemblance to the pit viper *Bothrops caribbaeus*.

#### *Boa sigma* (Smith, 1943)

**Taxonomy.** Originally described as *Constrictor constrictor sigma* (mistakenly attributed to M. A. Smith [1943] by McDiarmid et al. [1999]); Zweifel (1960) relegated it to the synonymy of *Boa constrictor imperator*. Card et al. (2016) recommended elevation to species level based largely on molecular data, while Suárez-Atilano et al. (2017) suggest that the species is further defined ecologically and geographically. No subspecies are recognized.

**Type Specimen.** An adult female (USNM 46484) from María Madre Island in the Tres Marías Islands, Nayarit, Mexico (H. M. Smith, 1943).

**Distribution.** The Pacific coast of Mexico west of the Isthmus of Tehuantepec (including three islands in the Tres Marías (Nayarit): María Madre, María Magdalena, and María Cleofas (Zweifel, 1960; Card et al., 2016; Suárez-Atilano et al., 2017).

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Chilabothrus* Duméril & Bibron, 1844

The genus *Chilabothrus* encompasses 13 recognized species restricted to the Greater Antillean Islands of Puerto Rico, Jamaica, Hispaniola, and the Puerto Rico Bank; as well as the Lucayan Archipelago (Bahamas and Turks and Caicos). These actively foraging nocturnal booids range in body size from  $<1 \text{ m}$  to  $\sim 4 \text{ m}$ , with larger species being habitat and dietary generalists and smaller species frequently specializing (Rodríguez-Robles and Greene, 1996; Reynolds et al., 2016c). Members of *Chilabothrus*

were considered to be congeneric with the genus *Epicrates* (e.g., Tolson, 1987), which is restricted to mainland Central and South America (and some continental islands). Phylogenetic analyses revealed that mainland *Epicrates* are phylogenetically sister to *Eunectes* (anacondas) and that West Indian representatives formed a monophyletic clade dating to the Miocene (Reynolds et al., 2013a). In addition to the recent elevation of the available name *Chilabothrus* for the West Indian clade, several taxonomic changes have occurred recently within the genus, including the elevation of three lineages to species (Reynolds et al., 2013a, 2018; Rodríguez-Robles et al., 2015), as well as the discovery of a previously unknown species (Reynolds et al., 2016a).

#### *Chilabothrus angulifer* (Bibron, 1840)

**Taxonomy.** Original name was *Epicrates angulifer*, generally attributed to Cocteau and Bibron (1838), though thought to be the description of Bibron (Smith and Grant, 1958) and occasionally given as Bibron 1843 (e.g., Henderson and Arias, 2001; Frynta et al., 2016). Genus was changed to *Chilabothrus* (Reynolds et al., 2013a). No subspecies are recognized.

**Type Specimen.** Lectotype MNIH N 3292 male, unknown locality.

**Distribution.** A species endemic to the island of Cuba and associated satellite islands (Sheplan and Schwartz, 1974; Schwartz and Henderson, 1991; Henderson and Arias, 2001). No subspecies are recognized, though a large degree of phenotypic variation is present across the island (Schwartz and Henderson, 1991; Henderson and Arias, 2001; Rodríguez-Cabrera et al., 2016).

**Conservation Status.** IUCN Red List Near Threatened (Day and Tolson, 1996). Although having a wide distribution and being locally common, this species is frequently persecuted when human encounters occur (Gundlach, 1880; Day and Tolson, 1996) and habitat loss has likely contributed to local



Figure 4. *Chilabothrus argentum* from Conception Island, Bahamas. Photo by R. Graham Reynolds, University of North Carolina Asheville.

declines (Tolson and Henderson, 1993). The species is also likely subject to mortality owing to vehicle strikes and invasive vertebrate predators (Rodríguez-Cabrera et al., 2016).

#### *Chilabothrus argentum* (Reynolds et al., 2016a)

**Taxonomy.** Discovered in situ in 2015, the species was named *Chilabothrus argentum*, as a lineage distinct from other members of the genus. No subspecies are recognized.

**Type Specimens.** Holotype MCZ R 193527, an adult female from Conception Island Bank, Bahamas.

**Distribution.** A species endemic to the Conception Island Bank, located in the central Bahamas Archipelago. No additional populations or subspecies are known. Previous species lists for the Conception Island Bank included *C. striatus* (now *C. strigilatus* Reynolds et al., 2013a) based on anecdotal suggestion of a boa present on the bank (Schwartz et al., 1978; Franz and Buckner, 1998; Buckner et al., 2012).

**Conservation Status.** IUCN Red List Critically Endangered (Reynolds, 2017) based on extremely small extent of occurrence (EOO, a polygon containing all known populations) and area of occupancy (AOO, the actual area occupied within the EOO polygon), likely declining population

size, and single known population (Reynolds et al., 2016a).

#### *Chilabothrus chrysogaster* (Cope, 1871)

**Taxonomy.** Originally described as *Homalochilus chrysogaster* (Cope, 1871), Stejneger (1904) moved it to *Epicrates*. It was subsequently moved into *Chilabothrus* with other West Indian *Epicrates* (Reynolds et al., 2013a). Two subspecies are recognized (Buden, 1975; see the *C. schwartzi* account).

**Type Specimen.** Holotype ANSP 10322, an adult of unknown sex. The holotype has since been lost, though presumably from “Turks Island,” a locality name that might have referred to either Grand Turk Island or South Caicos Island in the 19th century.

**Distribution.** A species from the southern Bahamas and Turks and Caicos archipelago, including Great Inagua Bank, Caicos Bank, and Turks Bank.

**Conservation Status.** IUCN Red List Near Threatened (Reynolds and Buckner, in press a) based on likely extirpations, habitat loss, and the threat of invasive vertebrate predators such as cats.

#### *Chilabothrus chrysogaster chrysogaster* (Cope, 1871)

**Taxonomy.** Considered to be a subspecies of *Epicrates striatus* by Stull (1935), and later as a subspecies of *E. chrysogaster* by Sheplan and Schwartz (1974).

**Type Specimen.** Holotype ANSP 10322, an adult of unknown sex. The holotype has since been lost.

**Distribution.** Largely restricted to islands on the Caicos Bank (Reynolds, 2011; Buckner et al., 2012; Reynolds, 2012; Reynolds and Gerber, 2012). On the Turks Bank, it is presently known from only a single small island (Reynolds and Niemiller, 2010; Reynolds et al., 2011).

**Conservation Status.** Species is listed on the IUCN Red List as Near Threatened (Reynolds and Buckner, in press a) owing to

predation by introduced vertebrates. This subspecies is likely extirpated from Grand Turk and South Caicos islands (Reynolds, 2011).

#### *Chilabothrus chrysogaster relicquus* (Barbour & Shreve, 1935)

**Taxonomy.** Originally described as *Epicrates relicquus* by Barbour and Shreve (1935; a misspelling of relicqus, meaning relict); it was considered a subspecies by Sheplan and Schwartz (1974).

**Type Specimen.** Holotype MCZ R 37891, an adult male from Sheep Cay, Inagua.

**Distribution.** Endemic to the Great Inagua Bank in the southern Bahamas archipelago (Schwartz and Henderson, 1991; Buckner et al., 2012; Reynolds, 2012).

**Conservation Status.** Little is known regarding the conservation status or natural history of this subspecies on Inagua, and no conservation assessments have been published.

#### *Chilabothrus exsul* (Netting & Goin, 1944)

**Taxonomy.** Described from a specimen collected on Abaco Island (Netting and Goin, 1944); subsequently placed in the genus *Chilabothrus* (Reynolds et al., 2013a). No subspecies are recognized.

**Type Specimen.** Holotype CM 21408, an adult male from Abaco Island.

**Distribution.** Little Bahamas Bank, though questionable records exist for Grand Bahama (Schwartz and Henderson, 1991; Reynolds et al., 2016b). Most records are from the Abaco islands.

**Conservation Status.** IUCN Red List Vulnerable (Reynolds and Buckner, 2016). Threats include invasive vertebrate predators, habitat loss, persecution, and significant road mortality (Reynolds et al., 2016b). A possible extirpation from Strangers Cay, Bahamas (Netting and Goin, 1944; Henderson and Powell, 2009) likely represents an extirpation of *Cubophis vudii* and not *C. exsul* (Netting and Goin, 1944).

***Chilabothrus fordii* (Günther, 1861)**

**Taxonomy.** Original name was *Pelophilus fordii*. Taxonomic changes included *Chilabothrus maculatus* Fischer 1888, *Epicrates fordii* Boulenger 1893 (subsequently referred to as *Epicrates fordii*), and *Chilabothrus fordii* Reynolds et al. 2013. Sheplan and Schwartz (1974) noted that the correct specific name is *fordii*, but that *fordi* should have been the proper name because the species is named for the individual Ford. According to Article 32.5 of the International Code for Zoological Nomenclature (ICZN), the original spelling does not constitute an “inadvertent error”; thus, the original specific epithet *fordii* stands. Subsequent authors have used both spellings, occasionally using the spellings interchangeably in separate treatments. Earlier works frequently used *fordi* (e.g., Schwartz, 1979; Henderson et al., 1987; Tolson, 1992; Tzika et al., 2008; Tolson and Henderson, 2011), while a mixture of older and most recent works recognize ICZN authority and use the spelling *fordii* (e.g., Tolson, 1987; Kluge, 1989; Reynolds et al., 2013a, 2014, 2015, 2016b,c). Three subspecies are recognized (Schwartz and Henderson, 1991; Tolson and Henderson, 1993; Henderson and Powell, 2004).

**Type Specimen.** Holotype BMNH 1946.1.1.55 (previously BMNH 1862.3.10.4), an adult female from the Dominican Republic (Wetherbee, 1987).

**Distribution.** A species endemic to the island of Hispaniola and some associated satellite islands (Schwartz, 1979; Schwartz and Henderson, 1991; Henderson and Powell, 2004).

**Conservation Status.** The species has been evaluated for listing on the IUCN Red List as Least Concern, though the listing is currently in review. Little is known regarding the conservation status of the species, though it can be locally common (Tolson and Henderson, 2011).

***Chilabothrus fordii fordii* (Günther, 1861)**

**Taxonomy.** Stull (1935) considered *Epicrates fordii* to be a subspecies of *E. inornatus*; that same year, Barbour considered it to be a subspecies of *E. fordii*, along with *E. f. monensis*. Sheplan and Schwartz (1974) eventually sorted out the taxonomy, recognizing the subspecies.

**Type Specimen.** Holotype BMNH 1946.1.1.55, an adult female from the Dominican Republic.

**Distribution.** Found in more xeric and low-lying regions across Hispaniola, excluding the Tiburon Peninsula, Île à Cabrit, and west of Cap-Haitien. Also found on a number of Hispaniolan satellite islands (Tolson and Henderson, 1993; Powell et al., 1999; Henderson and Powell, 2004).

**Conservation Status.** This subspecies is of unknown conservation status, though it can be locally common (Tolson and Henderson, 2011).

***Chilabothrus fordii agametus* (Sheplan & Schwartz, 1974)**

**Taxonomy.** Subspecies was described from a single male collected in 1960 by A.S. Rand and J.D. Lazell (Sheplan and Schwartz, 1974).

**Type Specimen.** MCZ R 62656, an adult male collected near Mole Saint-Nicholas, Département du Nord-Ouest, Haiti (Sheplan and Schwartz, 1974).

**Distribution.** Considered to occur in low-lying areas near the city of Mole Saint-Nicholas in the Pointe de Nord-Ouest, Haiti. The taxon might also occur east toward Cap-Haitien; little is known about this subspecies.

**Conservation Status.** This subspecies is of unknown conservation status.

***Chilabothrus fordii manototus* (Schwartz, 1979)**

**Taxonomy.** The original description of *Epicrates fordii manototus* was based on two

specimens obtained by R. Thomas in 1966 and D. A. Daniels in 1976 (Schwartz, 1979).

**Type Specimens.** Holotype CM 60519, an adult female from Île à Cabrit, Département de l'Ouest, Haïti (Schwartz, 1979).

**Distribution.** Endemic to Île à Cabrit, Département de l'Ouest, Haïti (Schwartz, 1979; Tolson and Henderson, 1993). Île à Cabrit is a small island <0.5 km off the coast of Haïti in Port-au-Prince Bay near the town of Aubry.

**Conservation Status.** This subspecies is of unknown conservation status, though of significant conservation concern, if indeed it is restricted to a single small ( $\sim 0.25 \text{ km}^2$ ) island.

#### *Chilabothrus gracilis* Fischer, 1888

**Taxonomy.** Originally described as *Chilabothrus gracilis*. Boulenger (1893) placed it in *Epicrates*, then back to *Chilabothrus* when resurrected by Reynolds et al. (2013a).

**Type Specimens.** Two syntypes in the ZMH, now destroyed (Sheplan and Schwartz, 1974); type locality “Cap Hayti” (=Cap-Haïtien), Département du Nord, Haïti.

**Distribution.** Widespread, but disjunct, on Hispaniola (Schwartz and Henderson, 1988; Henderson and Powell, 2002); can be locally common.

**Conservation Status.** The IUCN Red List assessment of this species is currently in review, with a recommended designation of Least Concern.

#### *Chilabothrus gracilis gracilis* Fischer, 1888

**Taxonomy.** First use of the trinomial was by Stull (1935) when she considered the taxon *monensis* to be a subspecies of *E. gracilis*; Sheplan and Schwartz (1974) provided a convincing argument that *monensis* was not a subspecies of *E. gracilis* (see *C. monensis* account).

**Type Specimens.** See *Chilabothrus gracilis* (above).

**Distribution.** Hispaniola, where found at scattered localities north of the Cul de Sac-

Valle de Neiba plain (Schwartz and Henderson, 1988).

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Chilabothrus gracilis hapalus* (Sheplan & Schwartz, 1974)

**Taxonomy.** Originally described as a subspecies of *Epicrates gracilis*.

**Type Specimen.** An adult male (MCZ R125602) from Camp Perrin, Département du Sud, Haïti.

**Distribution.** Hispaniola: in Haïti, the Tiburon (southwest) Peninsula east to Port-au-Prince and Jacmel; in the Dominican Republic, on the east coast of the Barahona Peninsula (Sheplan and Schwartz, 1974).

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Chilabothrus granti* (Stull, 1933)

**Taxonomy.** Originally described as a subspecies of *Epicrates inornatus*, Sheplan and Schwartz (1974) provided a new combination, identifying *granti* as a subspecies of *Epicrates monensis*. It had been informally referred to as a full species (e.g., Harvey and Platenberg, 2009; Platenberg and Harvey, 2010) owing to perceived uniqueness of this lineage as well as for conservation purposes. Rodríguez-Robles et al. (2015) provided a more thorough assessment for the recognition of *Chilabothrus granti* as a species distinct from *C. monensis*, further supported by Reynolds et al. (2015). No subspecies are recognized.

**Type Specimen.** An adult male from Tortola, British Virgin Islands (MCZ R33847).

**Distribution.** The Puerto Rico Bank: northeastern Puerto Rico, Cayo Diablo, Culebra, St. Thomas, Jost Van Dyke, Tortola, Great Camanoe, and perhaps Guana (Rodríguez-Robles et al., 2015).

**Conservation Status.** The IUCN Red List has designated this species Endangered, largely because of continuing habitat de-

struction (Tolson, 1996a; Platenberg and Boulon, 2011); see also Reynolds et al. (2015). Although not currently CITES listed, it presumably would be considered a CITES Appendix I species.

#### *Chilabothrus inornatus* (Reinhardt, 1843)

**Taxonomy.** Originally described as *Boa inornata* (Reinhardt, 1843), it was subsequently placed in the genera *Chilabothrus* (Duméril & Bibron, 1844) and *Epicrates* (Boulenger, 1893). Reynolds et al. (2013a) resurrected the genus *Chilabothrus* to encompass the Greater Antillean boids. No subspecies are recognized.

**Type Specimens.** Syntypes ZMUC R.5597, R.5598, and R.55101.

**Distribution.** Currently restricted to the main island of Puerto Rico (Rivero, 1998), though a few individuals likely exist on Culebra Island and could represent a recent introduction (R.G.R., personal observation).

**Conservation Status.** IUCN Red List Least Concern (Mayer and Tolson, 2010) and CITES Appendix I. Threats include invasive vertebrate predators, habitat destruction, persecution, road mortality, and historical collection for liver oil extraction (Reagan, 1984; Wiley, 2003; Mayer and Tolson, 2010; USFWS, 2011). This species is widely considered to have recovered from the near-complete deforestation of the island of Puerto Rico in the early 20th century. The island is now reforested in many areas, and boas are common in more remote situations (Puente-Rolón, 2012). This species is also now readily found near human habitation and can persist in small habitat patches (Puente-Rolón et al., 2013). The species was likely extirpated from Vieques Island.

#### *Chilabothrus monensis* (Zenneck, 1898)

**Taxonomy.** Originally described as *Epicrates monensis*. Stull (1935) considered it a subspecies of *E. gracilis*, but Sheplan and Schwartz (1974) provided sound evidence

for its recognition as distinct from *E. gracilis* (or *E. inornatus*). See also the *Chilabothrus granti* account. No subspecies are recognized.

**Type Specimens.** Five syntypes from Isla Mona in the ZMH (now destroyed; Sheplan and Schwartz, 1974).

**Distribution.** Isla de Mona.

**Conservation Status.** The IUCN Red List has designated this species Endangered (Tolson, 1996b); it is listed under CITES Appendix I (i.e., the most endangered and threatened with extinction). Threats include invasive vertebrate predators, especially cats, as well as habitat destruction owing to invasive pigs and rodents. As many as 70% of boas have scars or injuries caused by feral cats (Tolson, 1996b).

#### *Chilabothrus schwartzi* (Buden, 1975)

**Taxonomy.** Previously described as a subspecies of the Southern Bahamas boa (*Epicrates chrysogaster schwartzi*) by Buden (1975). This description was based on deceased animals and only one intact specimen (the holotype). The species was elevated based on the discovery of four wild individuals in 2018 and subsequent morphological and molecular phylogenetic analyses (Reynolds et al., 2018). No subspecies are recognized.

**Type Specimen.** Holotype LSUMZ 27500, a young adult female from Delectable Bay, Acklins Island.

**Distribution.** A newly-recognized boa species endemic to the Crooked-Acklins Bank, southern Bahamas. Known from four museum specimens (KU 260082-84; LSUMZ 27500) and four wild specimens (MCZ HO 28-31; Schwartz and Henderson, 1991; Reynolds, 2012; Buckner et al., 2012; Reynolds et al., 2018).

**Conservation Status.** This species has not been assessed based on IUCN Red List criteria. The species likely occurs across two large islands, though it is apparently rare or restricted to specific areas of these islands

(Reynolds et al., 2018). Threats to the species are unknown, but likely include persecution, road mortality, and introduced vertebrate predators.

#### *Chilabothrus striatus* (Fischer, 1856)

**Taxonomy.** Originally described as *Homalochilus striatus* by Fischer (1856); Boulenger (1893) provided the first use of *Epicrates striatus*. A number of subspecies have been described, but not all are currently recognized—three are recognized here. See McDiarmid et al. (1999) for a more complete synonymy.

**Type Specimens.** Syntypes, formerly in the ZMH, now destroyed; type locality Santo Domingo and St. Thomas, restricted to the vicinity of the city of Santo Domingo, Distrito Nacional, Dominican Republic (Sheplan and Schwartz, 1974).

**Distribution.** Widespread and common on Hispaniola and several satellite islands.

**Conservation Status.** This species has undergone IUCN Red List assessment, with a recommendation of Least Concern, which is currently in review.

#### *Chilabothrus striatus striatus* (Fischer, 1856)

**Taxonomy.** Originally described as *Homalochilus striatus* by Fischer (1856); Stull (1935) was the first use of the trinomial. The epithet *H. multisectus* (Cope, 1862) was subsumed into *C. s. striatus* (Sheplan and Schwartz, 1974).

**Type Specimens.** See *Chilabothrus striatus* (above).

**Distribution.** Widespread on Hispaniola north of the Cul-de-Sac-Valle de Neiba plain, in the Sierra de Baoruco, and on Ile de la Gonâve (Haiti) and Isla Saona (Dominican Republic).

**Conservation Status.** This taxon has not received an IUCN Red List assessment. It is often common where it occurs, especially in the Dominican Republic.

#### *Chilabothrus striatus exagistus* (Sheplan & Schwartz, 1974)

**Taxonomy.** Originally described as a subspecies of *Epicrates striatus*.

**Type Specimen.** An adult female (MCZ R 125603) from Département du Sud, Haiti.

**Distribution.** Western end of the Tiburon Peninsula and Île à Vache, Haiti; possibly intergrades with *C. s. striatus* near Jacmel, Département Sud-Est (Schwartz and Henderson, 1988).

**Conservation Status.** This taxon has not received an IUCN Red List assessment.

#### *Chilabothrus striatus warreni* (Sheplan & Schwartz, 1974)

**Taxonomy.** Originally described as a subspecies of *Epicrates striatus*.

**Type Specimen.** An adult female (MCZ R 125604) from Palmiste, Île de la Tortue, Haiti.

**Distribution.** Île de la Tortue, Haiti.

**Conservation Status.** This taxon has not received an IUCN Red List assessment. It has not been recently reported from the wild.

#### *Chilabothrus strigilatus* (Cope, 1862)

**Taxonomy.** Originally described as *Homalochilus strigilatus* (Cope, 1862), it was subsequently placed in the genus *Epicrates* (Barbour, 1904). It was subsequently relegated to a subspecies of the Hispaniolan boa (*C. striatus*) by Stull (1935) and Sheplan and Schwartz (1974) until the species was elevated by Reynolds et al. (2013a) based on molecular data and placed into the genus *Chilabothrus*. Five subspecies are recognized.

**Type Specimens.** Syntypes ANSP 10237 and 10239 from New Providence Island, Bahamas.

**Distribution.** Great Bahamas Bank.

**Conservation Status.** This species has been evaluated under IUCN Red List criteria and given a recommendation of Least Concern (Reynolds and Buckner, in press b).

*Chilabothrus strigilatus strigilatus* (Cope, 1862)

**Taxonomy.** See *C. strigilatus* account above.

**Type Specimens.** See *C. strigilatus* account above.

**Distribution.** The eastern Great Bahama Bank, from New Providence to Long Island (exclusive of Cat Island) and including Rose Island, Eleuthera, and the Exuma Cays (Schwartz and Henderson, 1991; Buckner et al., 2012).

**Conservation Status.** See *C. strigilatus* account above.

*Chilabothrus strigilatus ailurus* (Sheplan & Schwartz, 1974)

**Taxonomy.** This subspecies was first described by Sheplan and Schwartz (1974) based on material collected by G. Rabb in 1953 from Cat Island, Bahamas.

**Type Specimens.** Holotype AMNH 77015 from Cat Island, Bahamas.

**Distribution.** Endemic to Cat Island, Bahamas (Sheplan and Schwartz, 1974; Schwartz and Henderson, 1991; Buckner et al., 2012).

**Conservation Status.** See *C. strigilatus* account above.

*Chilabothrus strigilatus fosteri* (Barbour, 1941)

**Taxonomy.** This subspecies was first described by Barbour (1941) based on material collected from the Bimini Islands by R. Foster and J. Huntington.

**Type Specimen.** Holotype MCZ 46054 from North Bimini Island, Bahamas.

**Distribution.** Bimini Islands, Bahamas, on the western end of the Great Bahamas Bank. The subspecies is recorded from North Bimini, South Bimini, East Bimini, and Easter Cay (Schwartz and Henderson, 1991; Tolson and Henderson, 1993; Buckner et al., 2012).

**Conservation Status.** See *C. strigilatus* account above.

*Chilabothrus strigilatus fowleri* (Sheplan & Schwartz, 1974)

**Taxonomy.** This subspecies was first described by Sheplan and Schwartz (1974) based on material collected from the Andros Islands by Danny Fowler.

**Type Specimens.** Holotype MCZ 125605 collected in 1970 from Fresh Creek, North Andros (fide Sheplan and Schwartz, 1974).

**Distribution.** Endemic to the Andros Islands and Berry Islands, Bahamas.

**Conservation Status.** See *C. strigilatus* account above.

*Chilabothrus strigilatus mccraniei* (Sheplan & Schwartz, 1974)

**Taxonomy.** This subspecies was first described by Sheplan and Schwartz (1974) based on material collected from the Ragged Islands.

**Type Specimen.** Holotype UMMZ 118033 collected in 1957 by Robert Hanlon.

**Distribution.** Great Ragged Island, Little Ragged Island, and Margaret Cay in the Ragged Islands, Bahamas (Sheplan and Schwartz, 1974; Schwartz and Henderson, 1991; Buckner et al., 2012).

**Conservation Status.** See *C. strigilatus* account above. This subspecies is known to suffer from persecution and road mortality (R.G.R., personal observation).

*Chilabothrus subflavus* (Stejneger, 1901)

**Taxonomy.** Originally described as *Epirates subflavus*. No subspecies are recognized.

**Type Specimen.** An unsexed adult (~153 cm snout–vent length [SVL]), USNM 14507, from “Jamaica.”

**Distribution.** Jamaica, including Goat Island, though populations are now highly localized.

**Conservation Status.** Considered Vulnerable based on a 1996 IUCN Red List assessment (Gibson, 1996), though this is likely to be revised to Endangered given negative population trends (S. Koenig,

personal communication). It is listed in CITES Appendix I (i.e., the most endangered and threatened with extinction) and is listed on the Jamaica Wildlife Protection Act. The species is vulnerable to widespread habitat destruction, invasive predators, severe human persecution, road mortality, and the introduced and potentially toxic *Rhinelella marina* (Wilson et al., 2011; Newman et al., 2016).

### *Corallus* Daudin, 1803

Nine species comprise *Corallus*, a genus of arboreal boas. Members of the genus occur from southeastern Guatemala, through much of Central America (although the distribution can be disjunct), into South America, with a limited distribution west of the Andes in Colombia and Ecuador. East of the Andes the genus is widespread in the Guianas, Amazonia, and the Atlantic Forests of southeastern Brazil. Species also occur on continental islands (e.g., Isla Margarita, Trinidad, and Tobago), as well as oceanic islands (the St. Vincent and Grenada banks in the southern Lesser Antilles). The various species occur in a wide range of habitats; as they are arboreal, however, they are precluded from non-forested areas. Elevational distribution is from sea level to about 1,000 m. Species of *Corallus* range in size from ~1.2–2.1 m SVL. Diets of the various species include frogs, lizards, and a wide taxonomic range of birds and mammals (e.g., rodents, marsupials, and bats; Henderson, 2015). *Corallus* is sister to the *Epicrates-Eunectes* clade (e.g., Reynolds et al., 2014).

### *Corallus annulatus* (Cope, 1875)

**Taxonomy.** Originally described as *Xiphosoma annulatum*; Boulenger (1893) provided the first combination of *Corallus annulatus*. *Boa annulata* was used by Rendahl and Vestergren (1940, 1941); Peters (1957) used the current combination

after Forcart (1951) resurrected *Corallus*. No subspecies are recognized.

**Type Specimen.** A juvenile (USNM 32480) from “Costa Rica.”

**Distribution.** This species has a disjunct range that extends from extreme southeastern Guatemala, into northern Honduras; southeastern Nicaragua (in the Caribbean lowlands at elevations of 70–185 m, Sunyer and Köhler, 2010); northeastern Costa Rica where it reaches elevations to at least 745 m (Sosa et al., 2010) and perhaps as high as 1,000 m, and Panama, where it occurs on both Atlantic and Pacific versants in the central and southern portions of the country, and from sea level to about 400 m; (Jaramillo et al., 2010); to northern Colombia west of the Andes (Henderson, 2015).

**Conservation Status.** Considered a species of Least Concern on the IUCN Red List because of its widespread distribution (Sunyer and Köhler, 2016). Using IUCN Red List criteria, Sosa et al. (2010) gave this species an assessment of Endangered for Costa Rica.

### *Corallus batesii* (Gray, 1860)

**Taxonomy.** Originally described as *Chrysensis batesii*, but relegated to the synonymy of *Corallus caninus* by Boulenger (1893). Based on molecular (Vidal et al., 2005) and morphological data, Henderson et al. (2009) resurrected the species. No subspecies are recognized.

**Type Specimen.** A juvenile from the “Upper Amazons” in the BMNH (1859.12.28.12).

**Distribution.** Widely distributed in the Amazon basin. In Brazil north and south of the Rio Amazonas west of the Rio Negro, also in Amazonian Colombia, Ecuador, Peru, and Bolivia. It also occurs in northwestern Colombia north of the Andes, including the Río Magdalena valley. Elevational distribution is sea level to 1,100–1,200 m.

**Conservation Status.** According to the IUCN Red List this is a species of Least Concern because of its wide geographic distribution; it has no major threats, and it occurs in multiple protected areas (Rivas et al., 2016). It is a species that is popular in the pet trade, although ostensibly protected throughout most of its range.

***Corallus blombergii* (Rendahl & Vestergren, 1941)**

**Taxonomy.** Originally described as a subspecies of *Boa annulata*; it continued to be recognized as a subspecies by Peters (1957) as *Corallus annulata blombergi* and by Peters and Orejas-Miranda (1970) as *C. annulatus blombergi*. Based on morphological characters, it was elevated to species rank by Henderson et al. (2001). No subspecies are recognized.

**Type Specimen.** An adult specimen in the NRM (no. 3141), from “Eastern Ecuador, Rio Zamora” (Rendahl and Vestergren, 1941).

**Distribution.** Known from Ecuador in the western lowlands of the Andes. Its distribution extends from Esmeraldas to Azuay provinces but is very disjunct (Valencia et al., 2008; Henderson, 2015); it occurs at elevations below 200 m. Two specimens from extreme southwestern Colombia (Tumaco, Nariño) have recently been identified as *C. blombergii* (Pinto-Erazo and Medina-Rangel, 2018).

**Conservation Status.** The IUCN Red List has designated this species as Endangered due to its limited distribution ( $\sim 4,000 \text{ km}^2$ ) and because it is at risk from ongoing habitat loss (Cisneros-Heredia, 2016).

***Corallus caninus* (Linnaeus, 1758)**

**Taxonomy.** Originally described as *Boa canina*; it was briefly placed in the genus *Xiphosoma* (Fitzinger, 1843; Duméril and Bibron, 1844); Boulenger (1893) was first to use the combination *Corallus caninus*. Henderson et al. (2009) partitioned *C. caninus* into two species (*C. batesii* and *C. caninus*). No subspecies are recognized.

**Type Specimen.** NRM no. Lin. 8; type-locality is “Americae.”

**Distribution.** Guyana, Suriname, French Guiana, eastern and southern Venezuela (states of Bolívar and Amazonas), and northeastern Brazil north of the Rio Amazonas and north and east of the Rio Negro (in the states of Amapá, Pará, Roraima, and Amazonas); elevational distribution is from sea level to about 200 m.

**Conservation Status.** Considered a species of Least Concern on the IUCN Red List because of its large extent of occurrence and because there are no immediate threats to its habitat (Oubotar et al., 2016). It is a species that is popular in the pet trade, although ostensibly protected throughout much of its range.

***Corallus cookii* Gray, 1842**

**Taxonomy.** Originally described as *Corallus cookii*, it was relegated to subspecies rank by Stull (1935) as *Boa enydris cookii*; when Forcart (1951) resurrected *Corallus*, it became *C. e. cookii*; Roze (1966) recognized it as *C. hortulanus cookii*. Henderson (1997) elevated it to its former full species status as *C. cookii*. Recent molecular evidence (Colston et al., 2013; Reynolds et al., 2014) shows *C. cookii* nested within *C. hortulanus*; based on morphological characters and geography, Henderson (2015) continued to recognize it as a valid species. No subspecies are recognized.

**Type Specimen.** An 861-mm SVL male in the BMNH (1946.1.1.50); type locality “America” was amended to “West Indies” by Gray (1849); Henderson (1997) restricted it to St. Vincent in the Lesser Antilles.

**Distribution.** Endemic to the Lesser Antillean island of St. Vincent, where it is ecologically widespread. It has been encountered to at least 425 m above sea level (Henderson, 2015).

**Conservation Status.** The species has been assessed as Least Concern, though the listing is currently in review. We believe

that the species should likely be considered Near Threatened to Vulnerable based on Red List criteria. Recently, illegally collected individuals have become available on the Internet for the pet trade. The total area of its range is less than 350 km<sup>2</sup>.

### *Corallus cropanii* (Hoge, 1953)

**Taxonomy.** Described as the type species (*X. cropanii*) of a new genus (*Xenoboa*) by Hoge (1953). Based on its sister group relationship with *Corallus caninus*, and to avoid a paraphyletic taxon, Kluge (1991) placed *X. cropanii* in the genus *Corallus*. No subspecies are recognized.

**Type Specimen.** An adult male from Miracatu, São Paulo, Brazil; specimen in the IB, number 15200 (now presumably lost in the 2010 Instituto Butantan fire).

**Distribution.** Known only from Atlantic Forest in the state of São Paulo, southeastern Brazil.

**Conservation Status.** It is listed as Endangered on the IUCN Red List (Marques, 2010). In our estimation, it should be considered Critically Endangered, based on diminishing habitat, proximity of urban areas, and apparent low population density. A boa was recently found alive based on a successful citizen science initiative and extensively studied. Nevertheless, very little is known about this rare species.

### *Corallus grenadensis* (Barbour, 1914)

**Taxonomy.** Originally described as *Boa grenadensis*, Barbour (1914) subsequently relegated it to a subspecies of *B. cookii*; meanwhile, Stull (1935) synonymized it with *B. enydris cookii*; Barbour (1937) continued to recognize it as a subspecies of *B. cookii*. After Forcart (1951) untangled *Boa*, *Constrictor*, and *Corallus* and McDiarmid et al. (1996) did the same for *C. enydris/hortulanus*, Henderson (1997) resurrected *Corallus grenadensis* to full species status. Recent molecular evidence (Colston et al., 2013; Reynolds et al., 2014) shows *C. grenadensis*



Figure 5. *Corallus hortulanus* from Pará, Brazil. Photo by L. J. Vitt.

nested within *C. hortulanus*, though based on morphological characters and geographic isolation, Henderson (2015) continues to recognize it as a valid species. No subspecies are recognized.

**Type Specimen.** MCZ R7791 from St. George's (St. George Parish), Grenada.

**Distribution.** Islands on the Grenada Bank. It has been collected or observed on Bequia, Ile Quatre, Baliceaux, Mustique, Canouan, Mayreau, Union, Petit Martinique, Petit St. Vincent, Carriacou and Grenada. On Grenada, altitudinal distribution is from sea level to at least 530 m. Elevation is not likely to preclude *C. grenadensis* from occurring anywhere on the Grenadine Islands.

**Conservation Status.** This species has been given an IUCN Red List assessment of Least Concern, though that assessment is presently in review. Although it has a multi-island distribution, the total area of all the islands is ~400 km<sup>2</sup>. We believe that it could be considered Near Threatened to Vulnerable by Red List criteria. Recently, illegally collected individuals have become available on the Internet for the pet trade.

### *Corallus hortulanus* (Linnaeus, 1758)

**Taxonomy.** Originally described as *Boa hortulana*. The species has had a long, convoluted taxonomic history as, among

others, a species of *Boa*, *Corallus*, or *Xiphosoma*; often referred to as *Boa enydris* or *Corallus enydris*, and with many other synonyms. Its taxonomy was finally disentangled by McDiarmid et al. (1996); McDiarmid et al. (1999) provide an updated synonymy. No subspecies are recognized.

**Type Specimen.** NRM no. Lin. 7; although considered missing (Andersson, 1899), it apparently resides in the Swedish Museum of Natural History (McDiarmid et al., 1999); the type locality is “Ameriea.”

**Distribution.** The Guianas and Amazonia (southern Colombia, southern Venezuela, Ecuador, Peru, Bolivia, Brazil). The distribution in Brazil also includes Cerrado, mesic enclaves in Caatinga, sand dune areas in Caatinga (Rodrigues, 1996), Pantanal (Marques et al., 2005; Guedes et al., 2014), Atlantic rainforest to about 26°08'S, and Ilha Grande and Ilha Santo Amaro off southeastern Brazil. Altitudinal distribution is from sea level to about 915 m (Henderson, 2015).

**Conservation Status.** Considered a species of Least Concern on the IUCN Red List based on its broad geographic distribution, “relatively large population, lack of widespread threats, and occurrence in numerous protected areas” (Calderón et al., 2016:1). This is a popular species in the pet trade, although it is protected over most of its range.

#### *Corallus ruschenbergerii* (Cope, 1875)

**Taxonomy.** Originally described as *Xiphosoma ruschenbergerii* by Cope (1875). It was relegated to a subspecies of *Corallus cookii* (with an incorrect spelling, *ruschenbergi*, which has often been duplicated) by Boettger (1898); finally placed in the synonymy of *C. hortulanus cookii* by Roze (1966). Based on morphological evidence, Henderson (1997) resurrected it from the synonymy of *C. hortulanus* at species rank; molecular data have supported that resur-

rection (Colston et al., 2013; Reynolds et al., 2014). No subspecies are recognized.

**Type Specimen.** The holotype ANSP 10325 is from “Panama.”

**Distribution.** *Corallus ruschenbergerii* occurs from southern Costa Rica (sea level to 300 m; Sosa et al., 2010), through Panama from sea level to 525 m (Jaramillo et al., 2010), including the offshore islands of Isla del Rey, Isla Contadora, Isla de Cébaco, and Isla Suscantupu); in Colombia east of the Andes in the Llanos and adjacent foothills, and more or less north of the cordilleras Central and Oriental; and in Venezuela north of the Cordillera de Mérida and the Río Orinoco (and on Isla Margarita), and north and west of the Guiana Shield; also known from an intra-Andean locality (the Lake Maracaibo versant of the Cordillera de Mérida, Venezuela; Esqueda and La Marea, 2004); also on Trinidad and Tobago.

**Conservation Status.** Considered a species of Least Concern on the IUCN Red List on the basis of its large geographic range, “apparently large population size, occurrence in several protected areas, and apparently stable trend” (Aeosta Chaves et al., 2016:1). Using IUCN Red List criteria, Sosa et al. (2010) gave this species an assessment of Endangered for Costa Rica.

#### *Epicrates* Wagler, 1830

For more than 120 years, the genus *Epicrates* basked in relative stability, with a single widespread species (*E. cenchria*) on the Neotropical mainland and eight species inhabiting island banks in the Bahamas and on the Greater Antilles. Based on molecular phylogeny and historical biogeography, Reynolds et al. (2013a) determined that *Epicrates* was restricted to the mainland clade and they resurrected *Chilabothrus* for the West Indian clade. In a review of the *Epicrates cenchria* complex (based on meristic, morphological, and color pattern data), Passos and Fernandes (2008) elevated four taxa that had long been considered

subspecies of *E. cenchria* to species rank. Rivera et al. (2011) provided molecular support for the revision of Passos and Fernandes (2008). Currently, five species compose the genus, and all are restricted to the Neotropical mainland (Nicaragua to Argentina) and continental islands. The genus is ecologically widespread, and species occur in Amazonian and Atlantic forests, as well as xerophic Caatinga and grasslands. Species of *Epicrates* are largely ground dwelling and range in size from about 1,280 to 1,850 mm SVL (Passos and Fernandes, 2008). Their diets comprise a wide taxonomic range of ectothermic and endothermic vertebrates. Species of *Epicrates* are phylogenetically sister to *Eunectes* (e.g., Reynolds et al., 2013a).

#### *Epicrates alvarezi* Abalos, Baez, & Nader, 1964

**Taxonomy.** Originally described as a subspecies of *Epicrates cenchria* by Abalos et al. (1964), it was elevated to species status by Passos and Fernandes (2008). No subspecies are recognized.

**Type Specimen.** A presumably unnumbered adult female in the “Instituto de Animales Venenosos Jorge Washington Abaloz” from Forres, Department of Robles, Santiago Del Estero, Argentina (Passos and Fernandes, 2008).

**Distribution.** Chaco region of South America between southeastern Bolivia, western Paraguay, and northeastern Argentina. It is sympatric with *Epicrates crassus* in northwestern Paraguay and northern Argentina (Passos and Fernandes, 2008).

**Conservation Status.** This species has received an IUCN Red List assessment of Vulnerable, though the assessment is currently in review.

#### *Epicrates assisi* Machado, 1945

**Taxonomy.** Originally described as a subspecies of *Epicrates cenchria* by Machado (1945) but elevated to species status by

Passos and Fernandes (2008). No subspecies are recognized.

**Type Specimen.** An unnumbered adult male (presumably lost) in the Instituto Vital Brazil, from Campina Grande, Paraíba, Brazil (Passos and Fernandes, 2008).

**Distribution.** In Brazil, restricted to the Caatinga domain from the state of Piauí to southern Bahia and northern Minas Gerais. It is sympatric (but not syntopic) with *E. cenchria* but may occur syntopically with *E. crassus* (Passos and Fernandes, 2008).

**Conservation Status.** This species has not received an IUCN Red List assessment.

#### *Epicrates cenchria* (Linnaeus, 1758)

**Taxonomy.** Originally described by Linnaeus (1758) as *Boa cenchria*. Wagler (1830) described the new genus *Epicrates* and *E. cenchria* became the type species of the genus. Subsequently, many names have been associated with *E. cenchria*; McDiarmid et al. (1999) and Passos and Fernandes (2008) provide extensive synonymies. No subspecies are recognized.

**Type Specimen.** An adult in the NRM, no. Lin. 6; the type locality is Suriname.

**Distribution.** Forested Amazon Basin of Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Suriname, French Guiana, and Brazil; a disjunct population occurs in the Atlantic Forest from the Brazilian states of Alagoas to Rio de Janeiro (Passos and Fernandes, 2008).

**Conservation Status.** This species has not received an IUCN Red List assessment. It, along with some of its congeners, is considered a desirable species in the pet trade.

#### *Epicrates crassus* Cope, 1862

**Taxonomy.** Originally described as a full species by Cope (1862), it was relegated to a subspecies of *Epicrates cenchria* by Amaral (1929), then “considered” a full species by Lema (2002). No subspecies are recognized.



Figure 6. *Epicrates crassus* from Reserva Ecológica do IBGE, Brasília, Distrito Federal, Brazil. Photo by L. J. Vitt.

**Type Specimen.** An adult, USNM 12413, from Gardosa, Río Paraná, Paraguay.

**Distribution.** Open formations on the Andean slopes of Bolivia, grasslands of Argentina and Paraguay, and Brazilian Cerrado (in the states of Rondônia, Pará, Mato Grosso, Tocantins, Goiás, Minas Gerais, São Paulo, and grassland of Mato Grosso do Sul, Paraná, and Rio Grandes do Sul) (Passos and Fernandes, 2008).

**Conservation Status.** This species has not received an IUCN Red List assessment.

#### *Epicrates maurus* Gray, 1849

**Taxonomy.** Originally described as a full species, it was placed in the synonymy of *E. cenchria* by Boulenger (1893). Stull (1935) eventually recognized it as a subspecies of *Epicrates cenchria*; Chippaux (1986), however, considered it a full species, as did Gorzula and Señaris (1998). Nevertheless, McDiarmid et al. (1999) still considered it a subspecies of *E. cenchria*. Matz (2004) treated it as a full species and described two subspecies of *E. maurus* (both subspecies were subsequently placed in the synonymy of *E. maurus* by Passos and Fernandes, 2008). Passos and Fernandes (2008), in their review of the *E. cenchria* complex, considered it a full species. No subspecies are recognized.

**Type Specimen.** An adult male from Venezuela, BMNH 1946.1.10.40 (formerly BMNH 46.7.23. 2a + vi.6.3a).

**Distribution.** This species occurs in seasonally dry forest in Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, and northern Brazil, as well as on Trinidad, Tobago, and Isla Margarita; elevational distribution is 0–500 m. It may occur syntopically with *E. cenchria* where the savannah meets the forest (Passos and Fernandes, 2008).

**Conservation Status.** This species has received an IUCN Red List assessment of Least Concern, though the assessment is currently in review. Sosa et al. (2010), using IUCN criteria, gave it an assessment of Endangered in Costa Rica. Also using IUCN criteria, Jaramillo et al. (2010) gave an assessment of Least Concern for Panama.

#### *Eunectes* Wagler, 1830

This genus is composed of four species, and all are restricted to the South American mainland from Colombia and Venezuela to Argentina and the continental island of Trinidad. One species, *Eunectes murinus*, is one of the longest snakes in the world (to about 8.0 m, likely second in length to *Malayopython reticulatus* or *Python sebae*) and is certainly the most massive. All species are closely associated with water (e.g., rivers, swamps, “borrow” pits). Diets include a wide range of vertebrates, many of which are associated with aquatic habitats (turtles, crocodilians, wading birds, capybara; e.g., Rivas, 2000). All species are likely exploited for their hides. Species of *Eunectes* are phylogenetically sister to *Epicrates* (e.g., Reynolds et al., 2013a).

#### *Eunectes beniensis* Dirksen, 2002

**Taxonomy.** First described by Dirksen in 2002 and redescribed in Dirksen and Böhme (2005) based on color pattern

differences from *E. notaeus* and *E. deschauenseei*. No subspecies are recognized.

**Type Specimen.** An adult male, AMNH 101924, from Trinidad, Beni, Bolivia.

**Distribution.** Known from the northeastern departments of Beni, Santa Cruz, and Pando in Bolivia; it may also occur in nearby Brazil. Elevational range is ~115–350 m (Muñoz et al., 2016).

**Conservation Status.** The IUCN Red List has assessed the species as being of Least Concern based on its large estimated extent of occurrence (>45,000 km<sup>2</sup>; Muñoz et al., 2016). This species is collected for its skin and for its use as cooking fat; it is also killed because it feeds on chickens, dogs, and cats (Cortez et al., 2009). The Bolivian Government is presently assessing the feasibility of a sustainable harvest of anacondas within indigenous territories, and such activity would potentially affect the species.

#### *Eunectes deschauenseei* Dunn & Conant, 1936

**Taxonomy.** Described as a full species by Dunn and Conant (1936) based on a live individual. No subspecies are recognized.

**Type Specimen.** A female, ANSP 20891, “very probably” from Ilha de Marajó, Pará, Brazil (Dunn and Conant, 1936).

**Distribution.** Northeastern Brazil (Amapá and Pará) and French Guiana (Dirksen, 2002; Starace, 2013) and possibly in Suriname; possibly in narrow sympatry with *E. murinus*.

**Conservation Status.** The IUCN Red List considers the species Data Deficient (Dirksen, 2010), indicating a conservation concern but without supporting data.

#### *Eunectes murinus* (Linnaeus, 1758)

**Taxonomy.** Originally described as *Boa murina* by Linnaeus. When Wagler (1830) described the genus *Eunectes*, *B. murina* became the type species. Aside from Stull (1935) resurrecting the old Linnaean name *scytale* to replace *murinus*, and the epithet



Figure 7. *Eunectes murinus* from Estado Apure, Venezuela. Photo by César Luis Barrio Amorós.

*E. barbouri* being subsumed into *E. murinus* (Strimple et al., 1997; Dirksen, 2000), the species has had a remarkably stable taxonomic history. See McDiarmid et al. (1999), Dirksen (2002), and Dirksen and Böhme (2005) for a more complete synonymy. No subspecies are recognized.

**Type Specimen.** NRM no. Lin. 9; the type locality is “America.”

**Distribution.** South America east of the Andes: Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador, Peru, Bolivia, eastern Paraguay, and the continental island of Trinidad.

**Conservation Status.** This species has not received an IUCN Red List assessment.

#### *Eunectes notaeus* Cope, 1862

**Taxonomy.** Described by Cope in 1862, the species has had a stable taxonomic history. No subspecies are recognized.

**Type Specimen.** USNM 4707 (presumed lost) from “Paraguay River and confluent” (Cope, 1862).

**Distribution.** Southern South America including eastern Bolivia, southern Brazil, Paraguay, northeastern Argentina (Corrientes, Chaco, Entre Ríos, Formosa, Misiones and Santa Fe provinces; McDiarmid et al., 1999; Dirksen, 2002), and possibly Uruguay (Dirksen, 2002).

**Conservation Status.** This species has received an IUCN Red List assessment of Least Concern, though the assessment is currently in review. It has a history of being exploited for its hides (Waller et al., 2007).

## FAMILY CALABARIIDAE GRAY, 1858

### *Calabaria* Gray, 1858

Calabariidae is a monotypic family represented by a single extant species found in western Africa. *Calabaria reinhardtii* is a small oviparous species (<1.0 m SVL) that occurs in a variety of habitats, including primary and secondary swamp forest, cultivated fields, secondary dryland forest, and suburban environments; it is nocturnal, a specialized burrower, and often encountered underground, in leaf litter, or under cover objects. Its diet includes shrews and rodents (Luiselli and Akani, 1998; Luiselli et al., 2002). Calabariidae has been variously considered a pythonid (W. C. H. Peters, 1858), a boid, and a unique lineage, likely owing to a combination of unique and convergent morphological traits (Kluge, 1993). Recent molecular phylogenies suggest that Calabariidae is either nested within (Pyron et al., 2013; Reynolds et al., 2014) or sister to (Harrington and Reeder, 2017; Ruane and Austin, 2017) the booids; hence, we include it here as a booid family (fide Pyron et al., 2014), though we note that not all workers embrace this arrangement. The family Calabariidae was recognized by Pyron et al. (2014) to stabilize booid taxonomy in the face of inconsistent molecular and morphological phylogenetic hypotheses.

### *Calabaria reinhardtii* (Schlegel, 1848)

**Taxonomy.** Described by Schlegel (1848) as *Eryx reinhardtii*, the type of the genus was given as *Calabaria fusca* Gray 1858. The genus was referred to as both *Rhoptrura* and *Eryx* in the 19th century until Boulenger (1893) stabilized the monotypic genus as *C. reinhardtii*. Kluge (1993) placed



Figure 8. *Calabaria reinhardtii*, locality unknown (captive specimen). Photo by Mark O'Shea.

the species into *Charina* owing to shared morphological synapomorphies with North American *Lichanura* and *Charina*. No subspecies are recognized.

**Type Specimen.** The holotype is ZMB 1471, a specimen of unknown sex, likely from southeastern Ghana (Hughes and Barry, 1969).

**Distribution.** Widespread across western and central Africa, from the Democratic Republic of the Congo to Guinea-Bissau (Wallach et al., 2014).

**Conservation Status.** This species has not received an IUCN Red List assessment. It is not listed on the CITES appendices.

## FAMILY CANDOIIDAE PYRON ET AL., 2014

### *Candoia* Gray, 1842

The Pacific boas are a widely distributed group recognized here as constituting five species and 12 subspecies (though O'Shea, 2007, recognized 14 subspecies). They occur from the Moluccas (=Maluku) in the west, to the Palau Archipelago in the North, the Loyalty Islands in the south, and American Samoa in the east. Species of *Candoia* occur in a variety of habitats, including rainforests and coffee and coconut plantations (in discarded husk piles; O'Shea, 1996). They are of moderate size (0.5–1.5 m SVL), stout and ground-dwelling to more

slender and arboreal; viviparous; and the diet comprises mainly of lizards (primarily skinks) and murid rodents (Harlow and Shine, 1992). The genus *Enygrus* Wagler 1830 was originally used for these snakes, though a python (*Python regius*) was designated as the type specimen for the genus by Fitzinger (1843). This was resolved when Forcart (1951) recognized that *Candoia* Gray 1842 was the appropriate name for the South Pacific boas. It is worth noting that Gray (1842) initially provided the genus name *Candoia*, though the same author used *Enygrus* in subsequent work (Gray, 1849). Systematic revisions of the genus *Candoia* have been conducted at intervals. McDowell (1979) provided a detailed analysis of the biology, biogeography, and systematics of the group, recognizing the species *C. bibroni*, *C. carinata*, and *C. aspera*, though noting substantial regional variation in meristic characters. Smith et al. (2001) used morphological and squamation characters to further revise the *carinata* complex, recognizing two additional species (*C. paulsoni* and *C. superciliosa*) and 10 subspecies. Molecular phylogenetics have largely corroborated the proposed systematic revisions, based on both mitochondrial (Austin, 2000) and multilocus (Reynolds et al., 2014) datasets. Historical biogeographic analyses (Noonan and Chippindale, 2006; Noonan and Sites, 2010) have suggested an origin of the *Candoia* in the early Paleogene.

### *Candoia aspera* (Günther, 1877)

**Taxonomy.** The species was originally described as *Erebophis asper* (Günther, 1877), despite frequent incorrect assertions that the original name given by Günther (1877) was *Erebophis aspera*. The name was changed to *Enygrus asper* by Boulenger (1893) and to *Candoia aspera* by Forcart (1951). Thus the specific epithet is now *aspera*, which is the correct declension of the Latin feminine *Candoia*. See McDowell

(1979) and McDiarmid et al. (1999) for more detailed synonymies. Two subspecies are recognized.

**Type Specimen.** Holotype BMNH 1946.1.10.33 of unknown sex. The type locality is New Ireland Island (=Duke of York Island) in the Bismarck Archipelago.

**Distribution.** A species found below 1,300 m on the island of New Guinea and several nearby islands (e.g., Batanta, Misool, Waigeu); Biak and Japen islands; Seleo Island; Valise Island; Karkar Island; Umboi Island; islands in the Manus Group (Admiralty Islands); New Britain, Duke of York, New Ireland, and New Hanover in the Bismarck Archipelago (McDowell, 1979; Harlow and Shine, 1992; Austin, 2000; McCoy, 2015). Records from Bougainville Island in the Solomon Islands (Kinghorn, 1928) and Tokelau (Stull, 1935) are likely erroneous (McDowell, 1979).

**Conservation Status.** This species has not been assessed based on IUCN Red List criteria. The species is widespread, though is frequently killed when mistaken for venomous *Acanthophis* (O'Shea, 1996, 2007).

### *Candoia aspera aspera* (Günther, 1877)

**Taxonomy.** See the *Candoia aspera* account. It became the nominate subspecies of *Candoia aspera* with the description of *E. a. schmidti*.

**Type Specimen.** Holotype BMNH 1946.1.10.33, unknown sex, from New Ireland Island in the Bismarck Archipelago.

**Distribution.** This subspecies is endemic to the Bismarck Archipelago (New Ireland, Duke of York; M. O'Shea, in littoris, 4.iv.2018).

**Conservation Status.** This taxon has not been assessed based on IUCN Red List criteria, though it is widespread and locally common (O'Shea, 1996). It is likely persecuted (O'Shea, 1996).

### *Candoia aspera schmidti* (Stull, 1932)

**Taxonomy.** Described by Stull as *Enygrus asper schmidti* and subsequently recognized by Loveridge (1948). Later included in *Candoia* as *C. aspera schmidti* (Forcart, 1951).

**Type Specimen.** Holotype MCZ R29778, an adult female from near the Sepik River (=Kaiseriu Augusta River).

**Distribution.** This subspecies occurs on the island of New Guinea including several satellites (e.g., Jobi Islands, Raja Ampat Islands), New Britain, and the Admiralty Islands (M. O’Shea, in litteris, 4.iv.2018) and is generally found below 1,300 m elevation (O’Shea, 1996).

**Conservation Status.** This taxon has been assessed based on IUCN Red List criteria, though the assessment is still in review. It is widespread, locally abundant, and likely persecuted (O’Shea, 1996).

### *Candoia bibroni* (Duméril & Bibron, 1844)

**Taxonomy.** Originally described as *Tropidoboa de bibron* (Hombron and Jacquinot, 1842), formalized to *Enygrus bibroni* by Duméril and Bibron (1844), and occasionally referred to as *Enygrus bibronii* thereafter (e.g., Boulenger, 1886). Genus *Candoia* was resurrected by Forcart (1951), though the specific epithet is incorrectly given therein as *C. bibronii*. See McDowell (1979) and McDiarmid et al. (1999) for more detailed synonymies.

Specimens of this species were described as *Boa australis* by Montrouzier (1860). Boulenger (1893) split *E. bibroni* into *Enygrus australis* and *Enygrus bibronii*, and Roux (1913) used ventral counts to diagnose these as subspecies of *C. bibroni*. Forcart (1951) recognized these subspecies as *C. b. bibronii* and *C. b. australis*. Based on data in McDowell (1979), the subspecific status as currently recognized might be unwarranted by meristic characters. The subspecies were described based on ventral scale counts

(Roux, 1913), which are variable across the species’ range and do not correspond to geographic regions (McDowell, 1979). Although some geographic correlates exist for at least one skeletal characteristic (McDowell, 1979), this character does not form the basis of the subspecific description. Thus, we find insufficient reason to recognize the subspecies *C. b. bibroni* and *C. b. australis*.

**Type Specimens.** Syntypes MHN 1313, 3276–77, 61, and 61A, likely from the Fijian Archipelago, possibly from the island of Viti Levu (Stimson, 1969; McDowell, 1979).

**Distribution.** A species found below 1,200 m elevation across a number of island archipelagos in the South Pacific (Melanesia and Polynesia), from the Solomon Islands east to American Samoa (McDowell, 1979; Allison et al., 2012a; Zug, 2013). Considered to range into the Solomon Islands, then west to Makira, Rennell, and Bellona islands, but not found on Guadalcanal, Malaita, or further northwest in the archipelago (McCoy, 2015). Known from the Loyalty Islands (possibly introduced), but not mainland New Caledonia (Bauer and Sadlier, 2000), Vanuatu, the Fijian Archipelago (including Rotuma Island; M. O’Shea, in litteris, 4.iv.2018) the Wallis and Fortuna islands, Samoa, and American Samoa (McDowell, 1979; Allison et al., 2012a). Possible records from Tokelau (Stull, 1935) are likely erroneous, and records from Tonga are suspect (McDowell, 1979).

**Conservation Status.** This species has been assessed as Least Concern based on IUCN Red List criteria. It is widespread and does not appear to show evidence of population decline, though individuals are often killed, and some might be poached for the pet trade (Allison et al., 2012a). These boas are somewhat common in the Loyalty Islands, New Caledonia, and are occasionally eaten there (Bauer and Sadlier, 2000).

*Candoia carinata* (Schneider, 1801)

**Taxonomy.** Described as *Boa carinata* (Schneider, 1801). It became the type species for the genus *Candoia* Gray (1842). The name *Boa variegata* (Thunberg, 1807) was synonymized with *Candoia carinata* (Bauer and Wahlgren, 2001). The genus was changed to *Enygrus* (Duméril and Bibron, 1844) but restored to *Candoia* by Forcart (1951). See McDowell (1979) and McDiarmid et al. (1999) for more thorough synonymies. Two subspecies are recognized.

**Type Specimens.** Lectotype ZFMK 35503 from an unknown locality, though restricted to Amboina, Indonesia (McDowell, 1979; Böhme et al., 1998). Lectotype of *Boa variegata* (= *Candoia carinata* fide Bauer and Wahlgren, 2001) ZIUU 313, likely from the Moluccas (Bauer and Wahlgren, 2001; Smith et al., 2001).

**Distribution.** A species found on islands of eastern Indonesia to New Guinea and the Bismarck Archipelago (In den Bosch, 1985; Smith et al., 2001).

**Conservation Status.** This species has not been assessed based on IUCN Red List criteria. It is widespread and locally common, though it is likely persecuted (O'Shea, 1996).

*Candoia carinata carinata* (Schneider, 1801)

**Taxonomy.** Initially described as *Boa carinata* (Schneider, 1801). See *C. carinata* account.

**Type Specimen.** Lectotype ZFMK 35503 of unknown origin; see the *C. carinata* account.

**Distribution.** Distributed from the Sangihe Islands off Sulawesi (North Sulawesi Province) through the Maluku Islands (Maluku Province), including Tanimbar in the south and Seram in the north, through mainland New Guinea to the Owen Stanley Range (McDowell, 1979; O'Shea, 1996; Smith et al., 2001). Absent from Halmahera

(fide Smith et al., 2001). Found at elevations below 1,525 m on New Guinea (O'Shea, 1996).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

*Candoia carinata tepedeleni* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** First identified as *Enygrus carinatus* (Werner, 1899), later changed to *Candoia carinata carinata* (Stimson, 1969; affirmed by McDowell, 1979). This subspecies was described based on morphological and meristic characters (Smith et al. 2001).

**Type Specimens.** Holotype MCZ R72155, an adult male from Rabaul, New Britain, Bismarck Archipelago (Smith et al., 2001).

**Distribution.** Liki Island (Papua Province, West New Guinea) east through the Admiralty Islands and Bismarck Archipelago (New Britain and New Ireland islands) (McDowell, 1979; O'Shea, 1996; Smith et al., 2001).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

*Candoia paulsoni* (Stull, 1956)

**Taxonomy.** Apparently ignoring (or unaware of) Forcart's (1951) resurrection of *Candoia*, Stull (1956) described this taxon as a subspecies of *Enygrus carinata* (*E. carinatus paulsoni*). *Candoia carinata paulsoni* was elevated to a full species in the *C. carinata* complex by Smith et al. (2001). Six subspecies are recognized.

**Type Specimens.** Holotype MCZ R14521 from Ugi Island, Solomon Islands (Stull, 1956).

**Distribution.** A species with a disjunct range in eastern Indonesia including North Sulawesi Province (Talaud Islands) and the northern Malukus and from eastern New Guinea to the Solomon and Santa Cruz islands.

**Conservation Status.** This species has not been assessed based on IUCN Red List criteria. The species occupies a very large geographic range and occurs on many islands, where it can be locally common (O'Shea, 1996).

#### *Candoia paulsoni paulsoni* (Stull, 1956)

**Taxonomy.** Initially described as a subspecies, *Enygrus carinatus paulsoni*, of the *E. carinatus* complex (Stull, 1956) and later recognized as the nominotypical subspecies *C. p. paulsoni* (Smith et al., 2001).

**Type Specimen.** See *C. paulsoni* account above.

**Distribution.** Across the Solomon Islands archipelago, from the Feni Islands (New Ireland Province, Papua New Guinea) in the northwest to the Santa Cruz Islands in the southeast, except for Bougainville and Buka islands, where it is replaced by *C. p. vindumi* (Smith et al., 2001).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

#### *Candoia paulsoni mcdowellii* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** First described from New Guinea as part of Schlegel's (1872) *Boa carinata*; McDowell (1979) was first to recognize it as not *C. carinata*. The subspecies was recognized owing to meristic (squamation) characters (Smith et al., 2001).

**Type Specimens.** Holotype MCZ R111795, a female from Sogeri, Papua New Guinea (Smith et al., 2001).

**Distribution.** The subspecies is endemic to eastern Papua New Guinea, east and north of the PNG Highlands and Owen Stanley Range, as well as islands of the Milne Bay Province (Smith et al., 2001).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).



Figure 9. *Candoia paulsoni mcdowellii* from Milne Bay Province, Papua New Guinea. Photo by Mark O'Shea.

#### *Candoia paulsoni rosadoi* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** Based on specimens from Misima Island and originally referred to as *C. carinata* by McDowell (1979; part) and O'Shea (1996, as the "paulsoni" phase). The subspecies was recognized based on meristic (squamation) characters (Smith et al. 2001).

**Type Specimens.** Holotype AMS 124945, a male from Bwagaoia village, Misima Island (Smith et al., 2001).

**Distribution.** Endemic to Misima Island, Milne Bay Province, Papua New Guinea (Smith et al., 2001).

**Conservation Status.** This subspecies has not been assessed.

#### *Candoia paulsoni sadlieri* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** Specimens of this subspecies were originally identified as *Candoia carinata* (e.g., McDowell, 1979), or *C. c. paulsoni* (O'Shea, 1996). The subspecies was recognized based on meristic (squamation) characters (Smith et al., 2001).

**Type Specimens.** Holotype AMS 124877, a female from Guasopa, Woodlark Island.

**Distribution.** This subspecies is endemic to Woodlark Island, Milne Bay Province, Papua New Guinea (Smith et al., 2001).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

*Candoia paulsoni tasmai* Smith & Tepedelen, 2001 (in Smith et al., 2001)

**Taxonomy.** Like other subspecies in the *C. paulsoni* subcomplex, specimens of *C. p. tasmai* were considered to be *C. carinata* by Peters and Doria (1878), Stimson (1969), and McDowell (1979). The subspecies was recognized based on meristic (squamation) characters (Smith et al., 2001).

**Type Specimens.** Holotype USNM 215917, a male from Kampung Loloba, Halmahera.

**Distribution.** Endemic to Indonesia, where it occurs from the eastern arm of North Sulawesi (the Talaud Islands) through the northern Maluku Islands. This subspecies is isolated from other members of the *C. paulsoni* complex by ~800 km, though it is considerably closer to populations of *C. carinata* occurring in eastern Indonesia.

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

*Candoia paulsoni vindumi* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** Specimens of this subspecies were originally considered to be *C. carinata* by Sternfeld (1913) and McDowell (1979). The subspecies was recognized owing to meristic (squamation) characters (Smith et al., 2001).

**Type Specimens.** Holotype AMNH 92064, a female from Kunua, Bougainville Island.

**Distribution.** A subspecies endemic to Bougainville and Buka islands, central Solomon Islands. The subspecies possibly exists on satellites of Bougainville (Shortland, Ovau, and Fauro islands; Smith et al., 2001), but more likely they are inhabited by

the nominate subspecies (M. O'Shea, in littoris, 4.iv.2018).

**Conservation Status.** This subspecies has not been assessed, though it is likely persecuted (O'Shea, 1996).

*Candoia superciliosa* (Günther, 1863)

**Taxonomy.** Originally described as *Enygrus superciliatus* by Günther but was relegated to synonymy with *E. carinatus* by Boulenger (1893). Smith et al. (2001) resurrected *C. superciliosa* as part of their *C. carinata* complex. Two subspecies are recognized, and multilocus phylogenetic analysis suggests that these subspecies are minimally diverged (Reynolds et al., 2014).

**Type Specimens.** Syntypes BMNH 1946.1.16.47 (=BMNH 1863.10.2.7) and BMNH 1946.1.16.50 (=BMNH 1863.10.2.8) from the Palau Archipelago (island locality unknown).

**Distribution.** A species endemic to the Palau Archipelago (Smith et al., 2001).

**Conservation Status.** This species has been assessed as Least Concern based on IUCN Red List criteria. The species is common across multiple islands and in varied habitat types, though it is frequently killed (Allison et al., 2012b).

*Candoia superciliosa superciliosa* (Günther, 1863)

**Taxonomy.** See the *Candoia superciliosa* account.

**Type Specimens.** See the *Candoia superciliosa* account above.

**Distribution.** A subspecies endemic to islands of the main Palau Archipelago (Republic of Belau), from Peleliu Island north to Bebeldaob Island (including the Ngerukewid Islands; Wiles and Conry, 1990), below 200 m in elevation (Crombie and Pregill, 1999; Smith et al., 2001; Allison et al., 2012b).

**Conservation Status.** This subspecies is widespread and common, though threats include persecution (Allison et al., 2012b).

*Candoia superciliosa crombiei* Smith & Chiszar, 2001 (in Smith et al., 2001)

**Taxonomy.** Specimens of this subspecies were previously referred to as *Enygrus carinatus* (Sternfeld, 1913; Dryden and Taylor, 1969). Given the subspecific epithet *C. s. crombiei* based on number of ventral scales (Smith et al., 2001) and, presumably, on allopatry from the range of the subspecies *C. s. superciliosa*.

**Type Specimens.** Holotype USNM 521718, a juvenile male from Ngeaur Island, Palau.

**Distribution.** A subspecies endemic to Ngeaur Island, Palau (Smith et al., 2001).

**Conservation Status.** The conservation status of this subspecies is not known, though it is presently thought to be limited to a single island with an area of ~8 km<sup>2</sup> (Smith et al., 2001).

**FAMILY CHARINIDAE GRAY, 1849**

**Subfamily Charininae Gray, 1849**

***Charina* Gray, 1849**

Two species comprise the genus and they are restricted to southwestern Canada and the western United States. These are short (<1.0 m total length), stout-bodied boas that frequent grassland, woodland, and forest; they are good burrowers and often are encountered under cover objects (rocks, logs, bark). The diet of smaller (younger) individuals include squamate eggs and lizards (*Elgaria*, *Sceloporus*); larger (older) boas take birds and mammals (insectivores and rodents; Rodríguez-Robles et al., 1999). *Charina* and *Lichanura* are sister taxa to *Exiliboa* and *Ungaliophis* (Reynolds et al., 2014).

***Charina bottae* (Blaineville, 1835)**

**Taxonomy.** Originally described as *Tortrix bottae*; Gray (1849) described the genus *Charina* with *T. bottae* as the type species. It has had a fairly stable taxonomic history, with the only real deviation coming from Jan



Figure 10. *Charina bottae* from Kern County, California. Photo by Robert W. Hansen.

(1862), who placed *C. bottae* in the genus *Pseudoeryx*. See McDiarmid et al. (1999) for a complete synonymy. No subspecies are recognized.

**Type Specimen.** MNHN 730, from “Californie”; restricted to the “Coast Range, opposite Monterey, California” (Sehmidt, 1953).

**Distribution.** Southern British Columbia (Canada) to southern Utah, central Nevada, and southern California; Pacific Coast to western Montana and north-central Wyoming. Elevational range is from near sea level to about 3,050 m (Stebbins, 2003).

**Conservation Status.** The IUCN Red List identifies this as a species of Least Concern due to its wide range and presumed large population; it is unlikely to be declining fast enough for listing in a more threatened category (Hammerson, 2007).

***Charina umbratica* Klauber, 1943**

**Taxonomy.** Originally described as a subspecies of *Charina bottae*; Erwin (1974) first suggested elevating it to full species; Rodríguez-Robles et al. (2001) did elevate it to species rank based on morphological and molecular data. No subspecies are recognized.

**Type Specimen.** A (possibly immature) male, SDSNH 12101, from Fern Valley, near Idyllwild, Riverside Co., California.

**Distribution.** Southern California south of Mt. Pinos and the Tehachapi Mountains in San Bernardino and Riverside counties. Material from Mt. Pinos and the Tehachapi Mountains are possible *umbratica* × *bottae* intergrades (Stewart, 1977).

**Conservation Status.** This species has not received an IUCN Red List assessment.

### *Lichanura* (Cope, 1861)

A genus of small (<1 m SVL) species restricted to the extreme southwestern United States and around the Gulf of California in Mexico. Individuals are largely fossorial throughout most of the year, occupying rodent burrows. When surface active, largely in the Spring, individuals are frequently crepuscular, though they transition to nocturnal surface activity as the weather warms. Diet largely comprises mammals (mostly rodents; Rodríguez-Robles et al., 1999). Original descriptions of the genus recognized two species (Cope, 1861; Stejneger, 1889a; Klauber, 1931, 1933), though these were later collapsed into a single species and multiple subspecies (Ottley, 1978; Yingling, 1982; Gorman, 1985; Spiteri, 1988, 1992). The genus shows a wide range of morphological variation (Limburg et al., 2011), on which historical taxonomic divisions were based (Yingling, 1982), and molecular phylogenetic data suggest at least three (mitochondrial) lineages, two of which are presently recognized at the specific level (Wood et al., 2008). *Lichanura* has previously been synonymized with *Charina* (e.g., Kluge, 1993; Murphy and Aguirre-Léon, 2002), though we follow most modern interpretations in recognizing both genera.

### *Lichanura orcutti* Stejneger, 1889b

**Taxonomy.** Originally recognized as *Lichanura orcutti* (Stejneger, 1889b) and redescribed along with *L. simplex* by Stejneger (1889a). *Lichanura simplex* is now considered a junior synonym (Wood et al., 2008). The subspecies *L. trivirgata rose-*



Figure 11. *Lichanura trivirgata* from Bahia Los Angeles, Mexico. Photo by R. Graham Reynolds, University of North Carolina Asheville.

*ofusca* (Cope, 1868) has occasionally been considered a synonym of *L. orcutti* (Yingling, 1982). This species likely comprises at least two lineages (Wood et al., 2008). No subspecies are recognized.

**Type Specimens.** Holotype USNM 15503, an adult of unknown sex from San Diego County, USA.

**Distribution.** North of the Tijuana River watershed in San Diego County, California, and east to the Colorado River and Gila River drainages in Arizona (Wood et al., 2008). Closely contacts *L. trivirgata* near Chula Vista, California.

**Conservation Status.** This species is recently recognized based on mitochondrial DNA and has not been assessed by IUCN criteria. It is widespread and locally common, though coastal populations have likely been reduced or extirpated in areas of heavy development. Nevertheless, the species is capable of surviving in close proximity to development (Diffendorfer et al., 2005; Lemm, 2006). Some populations have likely been affected by collection for the pet trade (Parizek et al., 1996) or possibly by road mortality (Rosen and Lowe, 1994).

### *Lichanura trivirgata* Cope, 1861

**Taxonomy.** Originally described as *Lichanura trivirgata* (Cope, 1861), the species

has previously been recognized as *L. roseofusca* (Cope, 1868) and *Charina trivirgata*. The subspecies *L. trivirgata roseofusca* (Cope, 1868) and *L. trivirgata myriolepis* (Cope, 1868) are considered synonyms of *L. trivirgata* (Ottley et al., 1980; Wood et al., 2008). *Lichanura trivirgata gracia* was described based on presumed regional coloration (Klauber, 1931). No subspecies are recognized.

**Type Specimens.** Syntype ANSP 6698, specimen consists of just the skin.

**Distribution.** Wide ranging and locally abundant from south of the Tijuana and Otay watersheds to the tip of the Baja Peninsula and around the Sea of Cortés to coastal Sonora, Mexico. Occurs on continental islands off the Pacific coast of Mexico (Isla Cedros; Ottley, 1978) as well as islands in the Sea of Cortés (Murphy and Aguirre-Léon, 2002).

**Conservation Status.** This species has been assessed as Least Concern based on IUCN criteria (Hammerson et al., 2007). While locally abundant, some populations are likely threatened with collection for the pet trade (Mellink, 1993).

#### Subfamily Ungaliophiinae McDowell, 1987

##### *Exiliboa* Bogert, 1968b

*Exiliboa* is a monotypic genus restricted to southern Mexico. *Exiliboa placata* appears to be restricted to cloud forest, where it is frequently encountered under flat rocks. It is a small charinid (<0.5 m total length), and its diet might be confined to amphibian prey (frogs and salamanders; Campbell and Camarillo, 1992). *Exiliboa* and *Ungaliophis* are sister taxa to North American *Charina* and *Lichanura* (e.g., Reynolds et al., 2014).

##### *Exiliboa placata* Bogert, 1968b

**Taxonomy.** Described as the type species (*E. placata*) in a new genus (*Exiliboa*) by Bogert (1968b). No subspecies are recognized.



Figure 12. *Exiliboa placata* from Oaxaca, Mexico. Photo by J. A. Campbell.

**Type Specimen.** A female (“possibly immature”) in the AMNH 100000 from the headwaters of the Río Valle Nacional on the northern slopes of the Sierra de Juárez, Oaxaca, Mexico (elevation ~2,300 m; Bogert, 1968b).

**Distribution.** The Sierra de Juárez and near Totontepec in the Sierra Mixe, Oaxaca, Mexico, from 800 to at least 2,368 m (Campbell and Camarillo, 1992).

**Conservation Status.** According to the IUCN Red List, *E. placata* is Vulnerable due to its extent of occurrence (<20,000 km<sup>2</sup>); it is “known from only two locations and there is continuing decline in the extent and quality of its cloud forest habitat” (Canseco-Márquez and Flores-Villela, 2007:1).

#### *Ungaliophis* Müller, 1880

Two species comprise the genus *Ungaliophis*, and combined, they range from southern Mexico, through Central America, and into northwestern Colombia. They occur in tropical deciduous forest and lowland moist and wet forest to lower montane wet forest from near sea level to ~2,300 m. Both species are small (<675 mm total length) and largely arboreal (often associated with epiphytic vegetation) but may be encountered on the ground as well (Corn, 1974; Köhler, 2003; McCranie, 2011). Diet in nature includes birds and

bats (Dwyer, 2017; Solórzano and Carillo, 2017) and possibly frogs and lizards. *Ungaliophis* and *Exiliboa* are sister taxa to North American *Charina* and *Lichanura* (e.g., Reynolds et al., 2014).

#### *Ungaliophis continentalis* Müller, 1880

**Taxonomy.** Originally described as *Ungaliophis continentalis*. The name *Peropodum guatemalensis* Bocourt has caused some confusion regarding the genus *Ungaliophis* and this species, but it has been clarified by Stuart (1954) and McDiarmid et al. (1999). No subspecies are recognized.

**Type Specimen.** NMBA 427, possibly a female, from Retalhuléu (Department of Retalhuléu), Guatemala.

**Distribution.** Pacific coastal plain and highlands of southern Mexico (southeastern Chiapas), Pacific coastal plain of southwestern Guatemala, Honduras, and Nicaragua; elevational distribution from 100 m to about 2,300 m.

**Conservation Status.** This species is being considered for listing as Near Threatened under IUCN Red List criteria, although the account is currently in review. Acevedo et al. (2010) provided an IUCN category of Vulnerable for this species in Guatemala, as did Townsend and Wilson (2010) for Honduras and Sunyer and Köhler (2010) for Nicaragua.

#### *Ungaliophis panamensis* Schmidt, 1933

**Taxonomy.** Originally described as *Ungaliophis panamensis*. Bogert (1968a) provided evidence for placing *Ungaliophis danieli* from Colombia (Prado, 1940) in the synonymy of *U. panamensis*. No subspecies are recognized.

**Type Specimen.** An adult female in the USNM 54029 from Cerro Brujo, Colon Province, Panama (elevation 2,000 feet [610 m]; Schmidt, 1933).

**Distribution.** Southern Nicaragua, Costa Rica, Panama to northwestern Colombia



Figure 13. *Ungaliophis continentalis* from Chiapas, Mexico. Photo by J. A. Campbell.

from near sea level to about 2,100 m (Villa and Wilson, 1990).

**Conservation Status.** This species was assessed as an IUCN Red List species of Least Concern because of its wide distribution, stable population, and lack of major threats (Sunyer and Ibáñez, 2015). Sunyer and Köhler (2010), using IUCN methodology, gave this species an assessment of Vulnerable for Nicaragua. Similarly, Sosa et al. (2010), also using IUCN Red List criteria, provided an assessment of Endangered for this species in Costa Rica.

### FAMILY ERYCIDAE BONAPARTE, 1831

#### *Eryx* Daudin, 1803

The family Erycidae is a monogeneric group of relatively small (<1.0 m SVL) fossorial snakes. They occur in desert, near-desert, and dry woodland habitats; diet includes lizards, birds, and mammals (Rodríguez-Robles et al., 1999). They generally possess relatively small eyes, which can be oriented more dorsally rather than laterally in some species. A second genus (*Gongylophis* Wagler 1830) had been resurrected (McDowell, 1979; Tokar, 1995, 1996) and used to distinguish members lacking a mental groove (Tokar, 1995), but this arrangement rendered *Eryx* paraphyletic (Noonan and Chippindale, 2006;

Reynolds et al., 2014). *Eryx* as a group is understudied from a systematics perspective, and there is little agreement on the number of species and subspecies that should be recognized. For example, Pyron et al. (2014) recognize 13 species, while Uetz et al. (2017) recognize 12 species. These differences are owing to the lack of consensus regarding whether *E. vittatus* is a separate species. Here we recognize 13 species, including *E. vittatus* owing to slight distinctiveness in recent molecular phylogenies (Lynch and Wagner, 2010; Reynolds et al., 2014), and no subspecies.

#### *Eryx borrii* Lanza & Nistri, 2005

**Taxonomy.** Described from a single specimen based on a relatively higher ventral scale count than other Somali *Eryx* (Lanza and Nistri, 2005). No subspecies are recognized.

**Type Specimen.** Holotype BMNH 1900.11.28.4, a female from Biji, Somalia (Lanza and Nistri, 2005).

**Distribution.** A species presumably endemic to the vicinity of Biji, in northwestern Somalia, at an elevation of 400 m (Lanza and Nistri, 2005). It is similar in coloration to *E. somalicus* (fide Lanza and Nistri, 2005).

**Conservation Status.** This species has not been assessed based on IUCN Red List criteria. It is likely persecuted (Lanza and Nistri, 2005); presently only known from a single specimen.

#### *Eryx colubrinus* (Linnaeus, 1758)

**Taxonomy.** Originally described as *Anguis colubrina* (Linnaeus, 1758), the species was variously considered *Eryx thebaicus* (Reuss, 1834), *E. jaculus* (Jan and Sordelli, 1860–1866), and *E. rufescens* (Ahl, 1933). Flower (1933) considered *E. thebaicus* Stull 1932 conspecific with *E. colubrinus*. The subspecies *E. c. loveridgei* was recognized by Stull (1932) as a distinct lineage based on meristic and coloration differences from

populations in Kenya (Stull, 1932), though Tokar's (1996) assessment suggests that these characters are clinal and that no subspecies are warranted. Lynch and Wagner (2010) suggest some phylogenetic divergence in the putative subspecies, though that analysis was based on a supermatrix approach; hence, additional information would be needed to warrant phylogenetic support for these subspecies.

**Type Specimen.** Type specimen is lost, though it presumably was from Egypt (Flower, 1933).

**Distribution.** Widely distributed in northwest Africa (Niger, Chad, Egypt, North Sudan, Eritrea, Ethiopia) and east Africa (Kenya, Tanzania, Somalia, Djibouti), as well as western Yemen on the Arabian Peninsula (Parker, 1949; Marx, 1968; Largen, 1997; Wallach et al., 2014).

**Conservation Status.** Not assessed based on IUCN Red List criteria, but collected for the pet trade (Flower, 1933).

#### *Eryx conicus* (Schneider, 1801)

**Taxonomy.** Originally described as *Boa conica*, this taxon later formed the basis for the description of the genus *Gongylophis* (Wagler, 1830). *Gongylophis* is no longer recognized following molecular phylogenetic reconstruction of the Erycidae (Reynolds et al., 2014), and the species is considered to be within the genus *Eryx*. No subspecies are recognized.

**Type Specimen.** Syntype ZMB 1470, likely from southeast India (Stimson, 1969); a second syntype in “Museo Barbyensi” was unlocated (McDiarmid et al., 1999).

**Distribution.** South Asia, including Pakistan, India, Sri Lanka, Nepal, and Bangladesh (Srinivasulu and Das, 2008).

**Conservation Status.** Not assessed based on IUCN Red List criteria, but thought to be common in portions of the range (Srinivasulu and Das, 2008).

### *Eryx elegans* (Gray, 1849)

**Taxonomy.** Originally described as *Cusoria elegans* by Gray (1849), the species was placed in the genus *Eryx* by Blanford (1876). Analyses of morphology (Eskandarzadeh et al., 2013) and mitochondrial DNA (Rastegar-Pouyani et al., 2008) indicated that some *E. jaculus* had been misidentified as *E. elegans*, and that the two species might be conspecific in northern Iran. Further examination suggests that *E. elegans* is a distinct species in northern Iran and that the confusion likely is owing to an incomplete dichotomous key for these species (Zarrintab et al., 2017). No subspecies are recognized.

**Type Specimen.** Holotype is BMNH 1843.7.21.70 (previously IV.19.1a), a female from Afghanistan.

**Distribution.** A relatively small range encompassing the northern portions of Iran (Safaei-Mahroo et al., 2015) and Afghanistan and southern parts of Turkmenistan.

**Conservation Status.** Not assessed based on IUCN Red List criteria.

### *Eryx jaculus* (Linnaeus, 1758)

**Taxonomy.** Originally described as *Anguis jaculus* by Linnaeus (1758), this species was subsequently assigned to the genus *Eryx* by Daudin (1803). Some sources recognize multiple subspecies (e.g., Tokar and Obst, 1993; Safaei-Mahroo et al., 2015; Uetz et al., 2017), though others have pointed out that the species is generally treated as monotypic (Sindaco et al., 2000). Morphological analyses of *E. jaculus* and *E. elegans* in Iran have demonstrated some confusion regarding species boundaries (Eskandarzadeh et al., 2013), though molecular phylogenies show they are likely distinct lineages (Lynch and Wagner, 2010). See McDiarmid et al. (1999) for a more complete synonymy. No subspecies are recognized.

**Type Specimen.** Lectotype NRM Lin-12, an adult of unknown sex from Egypt. The holotype is likely lost (Kluge, 1993).



Figure 14. *Eryx jaculus* from Caesarea, Israel. Photo by Assaf Uzan.

**Distribution.** Southeastern Europe from Romania through the Balkan Peninsula; Mediterranean Islands including Sicily (In-sacco et al., 2015) and Aegean islands (Sindaco et al., 2000); Iran (Gholamifard et al., 2012; Kazemi et al., 2015; Safaei-Mahroo et al., 2015) to western Turkey and the eastern Mediterranean Levant (Albaba, 2016); northern Africa, including Egypt (Marx, 1968) and west to Morocco.

**Conservation Status.** Not assessed based on IUCN Red List criteria. Persecuted near human habitation (Flower, 1933).

### *Eryx jayakari* Boulenger, 1888

**Taxonomy.** Recognized as a distinct species largely owing to squamation (Boulenger, 1888), and easily distinguishable from *E. johnii* (Zarrintab et al., 2017); oviparity is also a distinguishing trait. *Eryx fodiens* is a synonym (Stull, 1935; Stimson, 1969). No subspecies are recognized.

**Type Specimen.** Holotype is BMNH 1946.1.7.99 (previously 1888.12.29.4), a female from Muscat, Oman.

**Distribution.** The Arabian Peninsula and southwestern Iran (Soorae et al., 2010; Safaei-Mahroo et al., 2015).

**Conservation Status.** Categorized on the IUCN Red List as Least Concern owing to wide distribution and lack of evidence for population decline (Behbehani et al., 2012).

### *Eryx johnii* (Russell, 1801)

**Taxonomy.** Originally described as *Boa johnii*. Synonyms include *Boa anguiformis* (Schneider, 1801), *Eryx indicus* (Schlegel, 1837), and *E. maculatus* (Hallowell, 1848). Occasionally misspelled as *E. johni* (e.g., Rastegar-Pouyani et al., 2008). No subspecies are recognized.

**Type Specimen.** Lectotype (illustration) designated by M. A. Smith (1943) from Tamil Nadu State, India (fide Wallach et al., 2014); subsequently lost (Stimson, 1969). Syntypes are unlocated (McDiarmid et al., 1999).

**Distribution.** Southwestern Asia from Iran (Latifi, 2000; Safaei-Mahroo et al., 2015) to the Indian subcontinent (Srinivasulu and Das, 2008).

**Conservation Status.** Not assessed based on IUCN Red List criteria, but thought to be common in portions of the range (Srinivasulu and Das, 2008). Recent anecdotal evidence suggests that the species is being overharvested and is likely in decline.

### *Eryx miliaris* (Pallas, 1773)

**Taxonomy.** Originally described as *Anguis miliaris*, the species was placed into the genus *Eryx* by Eichwald (1831). Based on molecular phylogenetic analysis, Reynolds et al. (2014) found that this species might be conspecific with *E. tataricus*, or at least that additional work remains to designate species boundaries and diagnostic morphological characters for identification. Following Wallach et al. (2014), we continue to recognize it here. Two subspecies have been described, the nominate *E. m. miliaris* and *E. m. nogaiorum* (Nikolsky, 1910). Both Eskandarzadeh et al. (2013) and Zarrintab et al. (2017) suggest that *E. miliaris* does not occur in Iran. Given the uncertainty regarding the epithet *E. miliaris* vis-à-vis *E. tataricus*, we suggest not recognizing these subspecies pending much needed focal study of this potentially wide-ranging species. See McDiarmid et al. (1999) for a more complete synonymy.

**Type Specimen.** Holotype is presumed lost (Stimson, 1969; Kluge, 1993). A lectotype, MNKNU 27350 from the Dagestan region of Russia, was designated by Vedmederya et al. (2009).

**Distribution.** Caucasus south around the Caspian Sea, east to western China and Mongolia (Wallach et al., 2014); possibly in Iran (Safaei-Mahroo et al., 2015), but see Eskandarzadeh et al. (2013) and Zarrintab et al. (2017).

**Conservation Status.** Not assessed based on IUCN Red List criteria.

### *Eryx muelleri* (Boulenger, 1892)

**Taxonomy.** Originally described as *Gongylophis muelleri* to distinguish it from *E. jaculus* (Boulenger, 1892), the species was referred to *Eryx* by the same author the subsequent year (Boulenger, 1893). Tokar (1995) continued to recognize *Gongylophis*, though molecular phylogenetic analysis of Erycidae suggests that the name renders *Eryx* paraphyletic and current studies no longer recognize *Gongylophis*. *Eryx muelleri* is an oviparous species, likely a derived condition (Lynch and Wagner, 2010). No subspecies are recognized.

**Type Specimen.** Holotype BMNH 1891.11.20.2, a male from southeastern Sudan (Boulenger, 1892).

**Distribution.** Western Africa, from Mauritania south to Benin (Ullendorff et al., 2010), east to southern Chad, and south to northern Cameroon and Central African Republic. Possibly absent from Sierra Leone (Trape and Baldé, 2014).

**Conservation Status.** Not assessed based on IUCN Red List criteria.

### *Eryx somalicus* Scortecci, 1939

**Taxonomy.** Originally described as *Eryx somalicus* (Scortecci, 1939), the species was briefly moved to the genus *Gongylophis* (Lanza, 1990). Early representatives were likely misclassified as *E. thebaicus* (Bou-

lenger, 1901; Parker, 1949). No subspecies are recognized.

**Type Specimen.** Syntypes MSNM 281, likely from near Mogadishu, Somalia (Scortecci, 1939).

**Distribution.** Somalia (Parker, 1949; Lanza, 1990) and neighboring portions of Ethiopia (Largen and Rasmussen, 1992; Largen and Sprawls, 2010).

**Conservation Status.** Not assessed based on IUCN Red List criteria.

#### *Eryx tataricus* (Lichtenstein, 1823)

**Taxonomy.** Originally described as *Boa tatarica*, it has variously been recognized as a separate species or as a subspecies of *E. miliaris* (e.g., Lambert, 2002). Based on molecular phylogenetic analysis, Reynolds et al. (2014) found that this species might be conspecific with *E. miliaris*, or at least that additional work remains to designate species boundaries and diagnostic morphological characters for identification. Following Wallach et al. (2014), we continue to recognize it here. Two subspecies have been described, the nominate *E. t. tataricus* (Lichtenstein, 1823) and *E. t. speciosus* (Tzarevsky, 1916), the latter of which is considered to occur in a small portion of the central part of the range in Pakistan (Khan, 2004). *Eryx speciosus* was recently recognized (Ananjeva et al., 2006), though without clear motivation or justification. Given the uncertainty regarding the epithet *E. tataricus* vis-à-vis *E. miliaris*, we suggest not recognizing these species or subspecies pending much needed focal study of this wide-ranging species.

**Type Specimen.** Lectotype ZMB 1461 (Bauer et al., 2002), an adult of unknown sex, likely from the Aral Sea region of Uzbekistan and Kazakhstan (Khan, 2002).

**Distribution.** From the western shore of the Caspian Sea through northern Iran (Safaei-Mahroo et al., 2015), south to Pakistan (Khan, 2004), and from western

Turkmenistan east through western China to southern Mongolia.

**Conservation Status.** Not assessed based on IUCN Red List criteria.

#### *Eryx vittatus* Chernov, 1959

**Taxonomy.** This species was long recognized as a subspecies of *E. tataricus*. It was elevated to species rank by Tokar (1989) based on comparative osteological data, though it continues to be recognized as a subspecies by some authors (e.g., Safaei-Mahroo et al., 2015). Recent molecular phylogenies have suggested that the lineage is evolutionarily distinct from both *E. tataricus* and *E. miliaris*; hence, it is recognized as a species by Pyron et al. (2014) and Wallach et al. (2014), and we recognize it here. No subspecies are recognized.

**Type Specimen.** Holotype ZISP 14009, a male from near Dushanbe, Tajikistan.

**Distribution.** Central Asia, from northern Iran (Safaei-Mahroo et al., 2015) through northern Afghanistan and Pakistan to Kyrgyzstan and extreme eastern China.

**Conservation Status.** Not assessed based on IUCN Red List criteria.

#### *Eryx whitakeri* Das, 1991

**Taxonomy.** Specimens of *Eryx* from the Western Ghats were considered *E. conicus* until *Eryx whitakeri* was described by Das (1991) owing to squamation and coloration differences. No subspecies are recognized.

**Type Specimen.** Holotype ZSI 24810, an adult female from Mangalore, Karnataka State, India (Das, 1991).

**Distribution.** Apparently endemic to southwestern India, known from coastal regions from Gujarat State south to Kerala State (Das, 1991; Whitaker and Captain, 2004).

**Conservation Status.** Not assessed based on IUCN Red List criteria.

## FAMILY SANZINIIDAE ROMER, 1956

*Acrantophis* Jan, 1860

The genus *Acrantophis* consists of two recognized species endemic to the island of Madagascar and satellites. These boas of moderate size (to ~3.0 m total length for *A. madagascariensis*) occur in forested habitats. They are largely ground dwelling, nocturnal, and prey primarily on mammals, including lemurs (Glaw and Vences, 2007; Gardner et al., 2013). *Acrantophis madagascariensis* is largely restricted to northern Madagascar, while *A. dumerili* is restricted to southern Madagascar. Nevertheless, a broad zone of overlap occurs across the west-central portion of the island (Vences and Glaw, 2003). While these species may be distinguishable based on head squamation characteristics (Guibé, 1949, 1958; Vences and Glaw, 2003), a phylogenetic analysis of the mitochondrial locus 16S (Vences and Glaw, 2003) suggested that the two species are paraphyletic. Additional work using multilocus genetic data further supports the paraphyly of these two species, with some individuals identified as *A. cf. dumerili* belonging either to a southern population of *A. madagascariensis* or to a separate lineage of *Acrantophis* in southern Madagascar (Orozco-Terwengel et al., 2008; Reynolds et al., 2014). Both species are listed on CITES Appendix I, which prevents international trade in live individuals or parts obtained from these species.

*Acrantophis dumerili* Jan, 1860

**Taxonomy.** Originally described as *Acrantophis dumerili*. Boulenger (1893) assigned it to *Boa* (and Barbour, 1918, to *Constrictor*), but Stull (1935) resurrected *Acrantophis*. It was again briefly placed in the genus *Boa* by Kluge (1991), based on cladistic analysis of morphological characters and historical biogeographic inference. The genus *Acrantophis* was again resurrected after molecular phylogenetic analysis of Neotropical and Malagasy lineages (Vences

et al., 2001). The species epithet is occasionally given as *A. dumerili* (e.g., Vences and Glaw, 2003), though this would be an incorrect representation of the epithet honoring the individual A. M. Duméril. No subspecies are recognized.

**Type Specimen.** Holotype was in the MSNM but was destroyed in 1943. Type locality was questionable, but likely Amboasary, Madagascar (Henkel and Schmidt, 2000).

**Distribution.** A species endemic to southern Madagascar south of Antananarivo (Vences and Glaw, 2003; Glaw and Vences, 2007). No subspecies are recognized, though phylogenetic analysis suggests that species boundaries and phylogeographic variation are not well characterized (Orozco-Terwengel et al., 2008). This species has been reported from Reunion Island (Guibé, 1958; Kluge, 1991), but these records (e.g., MNHN RA 0.8161) are in error (Vences and Glaw, 2003; Wallach and Glaw, 2009).

**Conservation Status.** This species is listed on CITES Appendix I but is assessed as Least Concern based on IUCN Red List criteria. The species is widespread and does not appear to show evidence of population decline, despite persecution and habitat loss, and is tolerant of disturbed habitats (Raxworthy et al., 2011a).

*Acrantophis madagascariensis* (Duméril & Bibron 1844)

**Taxonomy.** Described as *Pelophilus madagascariensis*. Boulenger (1893) assigned it to *Boa*, but Stull (1935) resurrected *Acrantophis*. It was again briefly placed in the genus *Boa* by Kluge (1991) based on cladistic analysis of morphological characters and historical biogeographic inference. *Acrantophis* was resurrected after molecular phylogenetic analysis of Neotropical and Malagasy lineages (Vences et al., 2001). No subspecies are recognized, though phylogenetic analysis suggests that species boundaries and phylogeographic variation in

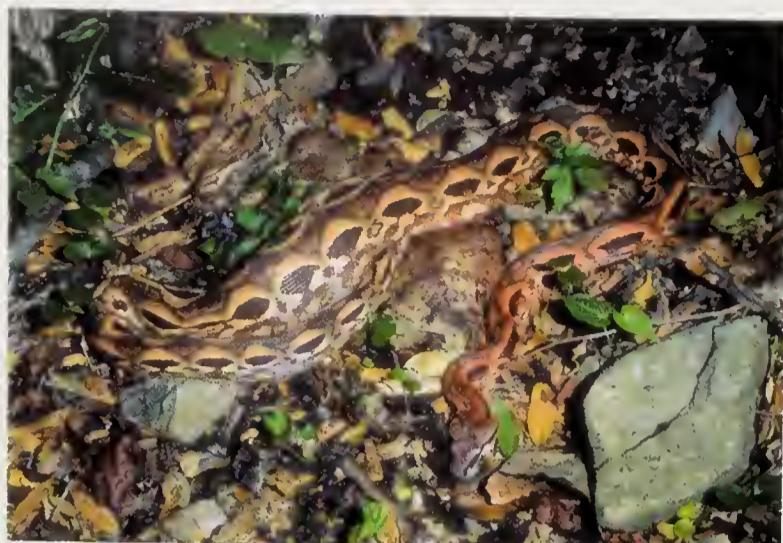


Figure 15. *Acrantophis madagascariensis* from Nosy Hara, Madagascar. Photo by Bill Love.

*Acrantophis* are not well characterized (Orozco-Terwengel et al., 2008).

**Type Specimens.** Syntypes MNHN RA 0.3133, MNHN RA 0.7275, MNHN RA 0.8636, all presumably from Mahajanga, Madagascar (Henkel and Schmidt, 2000).

**Distribution.** A species endemic to northern Madagascar and satellite islands (e.g., Nosy Be) north of Antananarivo, with some records along the west coast north of Morondava (Vences and Glaw, 2003; Glaw and Vences, 2007).

**Conservation Status.** This species is listed on CITES Appendix I but is assessed as Least Concern based on IUCN Red List criteria. The species is widespread and does not appear to show evidence of population decline (Raxworthy et al., 2011b).

#### *Sanzinia* Gray, 1849

The genus *Sanzinia* consists of two species, recognized herein, endemic to the island of Madagascar and satellites. These are moderate-sized boas (to ~2.5 m total length) that occur in primary and secondary forests, as well as heavily disturbed areas. They occur at ground level as well as in trees, are nocturnal, and their diet consists largely of mammals, including lemurs (Glaw and Vences, 2007; Eberle and Kappeler, 2008). *Sanzinia madagascariensis* is largely restricted to eastern Madagascar, while *S. volontany* is restricted to western Madagas-

car. Both species occur at elevations up to 1,300–1,600 m (Henkel and Schmidt, 2000; Glaw and Vences, 2007; Vences et al., 2011). A small contact zone is potentially present southwest of Toalagnaro in extreme southeastern Madagascar (Vences and Glaw, 2003). The two species are distinguishable based on geographic location, as well as coloration, with *S. volontany* being largely brown and lacking the green-colored scales characteristic of *S. madagascariensis*. A number of studies have recognized the evolutionary distinctness of *S. madagascariensis* and *S. volontany* based on mitochondrial and multilocus phylogenetic analyses (Vences and Glaw, 2003; Glaw and Vences, 2007; Orozco-Terwengel et al., 2008; Reynolds et al., 2014). The genus is listed on CITES Appendix I, which prevents international trade in live individuals or parts obtained from these species.

#### *Sanzinia madagascariensis* (Duméril & Bibron, 1844)

**Taxonomy.** Described originally as *Xiphosoma madagascariensis* (Duméril & Bibron 1844), the species was assigned to *Sanzinia* (Gray, 1849). Boulenger (1893) placed it in *Corallus*, but Stull (1935) brought it back to *Sanzinia*. It was subsequently placed in the genus *Boa* by Kluge (1991) based on cladistic analysis of morphological characters and historical biogeographic inference. The genus *Sanzinia* was resurrected following molecular phylogenetic analysis of Neotropical and Malagasy lineages (Vences et al., 2001). No subspecies are recognized.

**Type Specimens.** Syntypes MNHN RA 43 and MNHN RA 7329, likely from Nosy Be Island, Madagascar (Duméril and Duméril, 1851), though also given as from Ankaranana, Madagascar (Henkel and Schmidt 2000). A third possible syntype is ZMB 6400 (Bauer et al., 2002; Wallach et al., 2014).

**Distribution.** A species endemic to eastern Madagascar (Henkel and Schmidt, 2000; Glaw and Vences, 2007) and some

satellites (e.g., Nosy Boraha = Île Sainte-Marie).

**Conservation Status.** This species is listed on CITES Appendix I and is assessed as Least Concern based on IUCN Red List criteria. The species is widespread across eastern Madagascar and occurs in a variety of natural and modified habitats (Henkel and Schmidt, 2000; Vences and Glaw, 2003; Glaw and Vences, 2007). It is occasionally collected for the pet trade (Vences et al., 2011).

#### *Sanzinia volontany* Vences & Glaw, 2003

**Taxonomy.** Initially recognized as the subspecies *Sanzinia madagascariensis volontany* (Vences and Glaw, 2003). The lineage has been shown to be genetically distinct (Orozco-Terwengel et al., 2008; Reynolds et al., 2014) and somewhat phenotypically diagnosable (Vences and Glaw, 2003) from eastern Madagascar *S. madagascariensis*. No subspecies are recognized.

**Type Specimens.** Holotype ZSM 804/2001, an adult male from Ankarafantsika Reserve (Vences and Glaw, 2003).

**Distribution.** A species endemic to western Madagascar and some satellites (e.g., Nosy Komba) (Henkel and Schmidt, 2000; Glaw and Vences, 2007; Bora et al., 2010).

**Conservation Status.** The genus is protected under CITES Appendix I, though the species is not currently assessed under IUCN Red List criteria. The species is widespread across western Madagascar and occurs in a variety of natural and modified habitats (Henkel and Schmidt, 2000; Vences and Glaw, 2003; Glaw and Vences, 2007). It is occasionally collected for the pet trade (Vences et al., 2011).

### CONSERVATION

Despite some species of booids being among the most iconic of reptiles in general and perhaps including some of the most commercially sought-after species of snakes

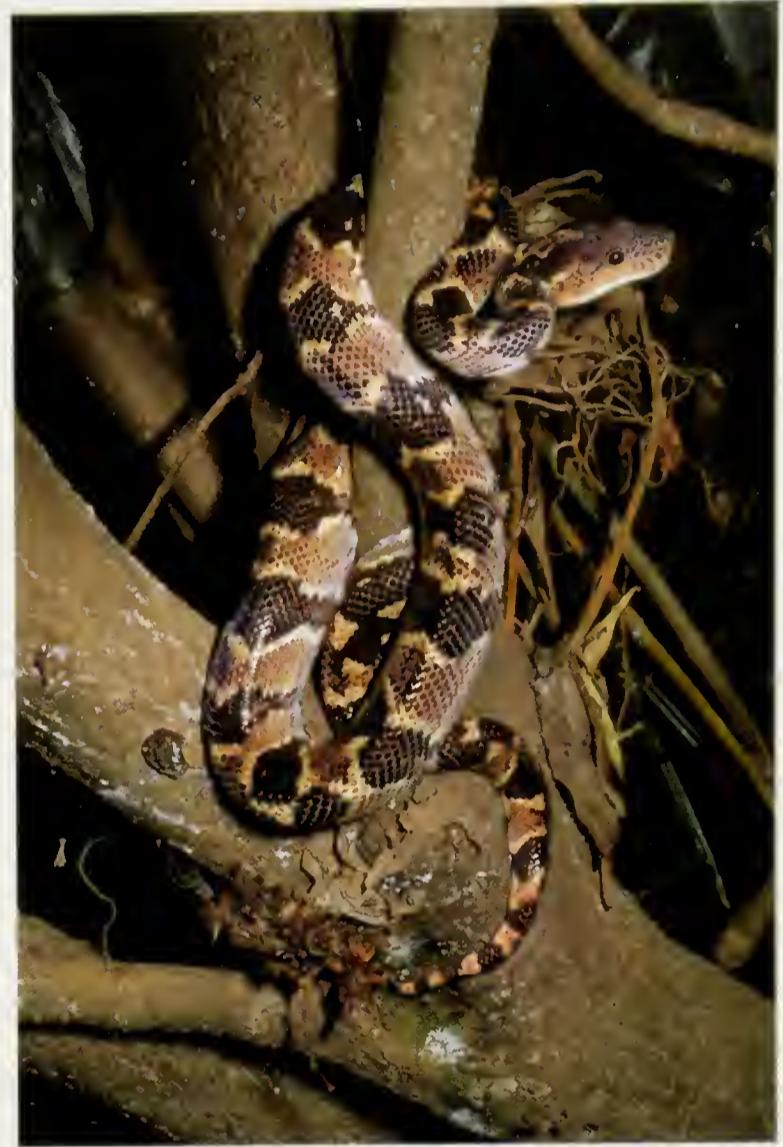


Figure 16. *Sanzinia volontany* from Tsingy de Bemaraha, Madagascar. Photo by Bill Love.

(e.g., *Boa constrictor*, *Corallus caninus*), only 59% of the 66 species have received IUCN Red List assessments (Table 3). Of those that have received assessments, 25 (37.9%) were designated Least Concern (i.e., species that are widespread and abundant). Only three species (*Chilabothrus angulifer*, *C. chrysogaster*, and *Ungaliophis continentalis*) are considered Near Threatened (i.e., close to qualifying for one of the threatened categories), and four (*Chilabothrus exsul*, *C. subflavus*, *Epicrates alvarezi*, and *Exiliboa placata*) are considered Vulnerable (i.e., considered to be facing a high risk of extinction in the wild). Five species (*Boa orophias*, *Chilabothrus granti*, *C. monensis*, *Corallus blombergii*, and *C. cropanii*) have been assessed as Endangered (i.e., considered to be facing a

TABLE 3. SUMMARY OF IUCN RED LIST ASSESSMENTS<sup>a</sup> FOR EACH FAMILY AND GENUS (NUMBER OF SPECIES). ASTERISKS INDICATE ACCOUNTS THAT ARE STILL IN REVIEW.

| Family and Genus (No.)   | NE | LC | NT | VU | EN | CR | DD |
|--------------------------|----|----|----|----|----|----|----|
| Boidae (36)              | 8  | 16 | 2  | 3  | 5  | 1  | 1  |
| <i>Boa</i> (5)           | 3  | 1° | —  | —  | 1° | —  | —  |
| <i>Chilabothrus</i> (13) | 1  | 5° | 2° | 2  | 2° | 1  | —  |
| <i>Corallus</i> (9)      | —  | 7° | —  | —  | 2  | —  | —  |
| <i>Epicrates</i> (5)     | 3  | 1° | —  | 1° | —  | —  | —  |
| <i>Eunectes</i> (4)      | 1  | 2° | —  | —  | —  | —  | 1  |
| Calabariidae (1)         | 1  | —  | —  | —  | —  | —  | —  |
| <i>Calabaria</i> (1)     | 1  | —  | —  | —  | —  | —  | —  |
| Candoiidae (5)           | 3  | 2  | —  | —  | —  | —  | —  |
| <i>Candoia</i> (5)       | 3  | 2  | —  | —  | —  | —  | —  |
| Charinidae (7)           | 2  | 3  | 1  | 1  | —  | —  | —  |
| <i>Charina</i> (2)       | 1  | 1  | —  | —  | —  | —  | —  |
| <i>Lichanura</i> (2)     | 1  | 1  | —  | —  | —  | —  | —  |
| <i>Exiliboa</i> (1)      | —  | —  | —  | 1  | —  | —  | —  |
| <i>Ungaliophis</i> (2)   | —  | 1  | 1° | —  | —  | —  | —  |
| Erycidae (13)            | 12 | 1  | —  | —  | —  | —  | —  |
| <i>Eryx</i> (13)         | 12 | 1  | —  | —  | —  | —  | —  |
| Sanziniidae (4)          | 1  | 3  | —  | —  | —  | —  | —  |
| <i>Acrantophis</i> (2)   | —  | 2  | —  | —  | —  | —  | —  |
| <i>Sanzinia</i> (2)      | 1  | 1  | —  | —  | —  | —  | —  |
| Totals                   | 27 | 25 | 3  | 4  | 5  | 1  | 1  |

<sup>a</sup> NE = Not Evaluated; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; DD = Data Deficient.

very high risk of extinction in the wild). The most endangered boa species globally (*Chilabothrus argentum*) is listed as Critically Endangered (i.e., considered to be facing an extremely high risk of extinction in the wild).

With two exceptions (*E. placata* and *U. continentalis*, both family Charinidae, subfamily Ungaliophiinae), all of the species that have received IUCN assessments that are not Least Concern or Data Deficient belong to the Boidae, a family of 36 species in the Neotropics (the Neotropical mainland and associated islands plus the West Indies). *Boa orophias* (St. Lucia) and all the *Chilabothrus* have island distributions, and the two species of *Corallus* have very restricted distributions on the South American mainland. Many islands and island archipelagos are among the world's biodiversity hotspots (e.g., the Caribbean, Madagascar, Polynesia-Micronesia; Mittermeier et al., 2011), and islands harbor a high percentage of the Booidae (37.9% of the species and 81.8% of the

subspecies). Perhaps not surprisingly, then, it is the island-restricted species that have most often received IUCN and CITES assessments (CITES Appendix I; IUCN Near Threatened to Critically Endangered) suggesting or indicating strong concerns for those species. Crucially, very little is apparently known about the conservation status of the Erycidae, with only 1 of the 13 species receiving an IUCN listing of Least Concern (*E. jayakari*). Given our occasionally problematic understanding of species boundaries and distributions in this group, further systematic and conservation study is greatly needed.

There are occasional discrepancies between the IUCN assessments and those of CITES. Several species that received IUCN assessments of Least Concern are listed under CITES Appendix I (both species of *Acrantophis*, *Chilabothrus inornatus*, and *Sanzinia madagascariensis*). Similarly, the range-wide IUCN assessments are sometimes at odds with an assessment (for which

IUCN criteria were employed) for a particular country. We have noted those discrepancies in the species accounts.

It is worth noting that, aside from distributions (many in biodiversity hotspots), general habitat, fortuitous field observations on diet, predation, reproduction, or laboratory-based analyses of diet or reproduction, we know remarkably little about the ecology (or natural history) of most species of booids. Fewer than 20% have been the focus of prolonged, dedicated field studies and nearly all the species that have been the focus of such work are members of the Neotropical Boidae (e.g., *Boa imperator*, *Chilabothrus angulifer*, *C. chrysogaster*, *C. granti*, *C. monensis*, *Corallus grenadensis*, *C. cropanii*, *Eunectes murinus*, *E. notaeus*) and North American Charinidae (*Charina bottae*, *Lichanura trivirgata*); a lone exception is the African calabariid *Calabaria reinhardtii*. The world's boas face multiple challenges to their survival and persistence. These include habitat loss and alteration, introduced predators (e.g., cats, dogs, mongooses), accidental killing (vehicular traffic on roads), intentional killing, restricted population sizes and ranges, climate change, natural disasters (hurricanes, typhoons, volcanic eruptions), environmental pollution, depleted or shifting prey bases, and commercial and cultural exploitation (with thousands exported from their countries of origin for the pet or skin trade; Montgomery et al., 2015).

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Photo on the front cover:

Adult female *Chilabothrus inornatus* (Boidae) from Arecibo, Puerto Rico. Photograph by R. Graham Reynolds, UNC Asheville.

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